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THE UNIVERSITY OF ALBERTA

STUDIES OF GEOGRAPHICAL POPULATIONS

OF

TRIBOLIUM CASTANEUM

BY



MOHAMED HANI SOLIMAN

A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Studies of Geographical Populations of Tribolium castaneum" submitted by Mohamed Hani Soliman, M.Sc., in partial fulfilment of the requirements for the degree of Master of Science.



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ABSTRACT

Twelve populations of T. castaneum from different geographical localities throughout the distribution of the species were studied. All populations were reared in standard media under a controlled environment at 33°C and 70% R.H.

Significant population differences were observed for 13-day larval, pupal and adult weight; pupation and adult emergence times; and duration period and total productivity (number of offspring of all stages). Duration of pupal stage was relatively constant among populations. Population differences were noted in growth curves derived from 13-day larval, first-day pupal and adult weights.

Phenotypic variation within populations was higher for productivity traits and larval weight than for pupal and adult weights or developmental times. Differences in phenotypic variation among populations were observed for all traits, with larval weight and productivity traits showing higher variation among populations than the other traits.

Relationships between the traits were examined in terms of phenotypic correlations and regressions. Highly significant positive correlations were observed for pupal weight with adult weight, pupation time with adult emergence time, and period of productivity with total productivity. Negative phenotypic correlations of larval weight with pupation time, and larval weight with adult emergence time were also observed.

Relationships of observed population differences with environmental latitude and average annual isotherm were obtained. These relationships were interpreted in regard to the existence of geographical clines.

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INTRODUCTION

Geographical variation studies have contributed to the clarification of the adaptation of local populations to their environments. The large size of their populations , their ease of collection, and their amenability to morphological, physiological, genetical and cytological studies of the same species, have made insects a highly suitable animal group for such investigations. Drosophila has been the most favourable of the many species which have been studied. However, Tribolium castaneum, a widely distributed species has several desirable properties which suggests its suitability for geographical variation studies.

T. castaneum can be reared on a simple medium from which all of its developmental stages can be separated with minimum disturbance to the organism. Several generations can be observed within a reasonable length of time, as the developmental period from egg to emerging adult is approximately one month under optimum conditions. Extensive ecological and rapidly expanding genetical information is available.

The object of the present investigation was to obtain information regarding different components of fitness in different geographical populations of T. castaneum. Such components of fitness represent an essential evidence of population adaptation in natural environments. However, T. castaneum because of its distribution by man and its existence in semi-controlled environments, may not be expected to show geographical variation. Thus the question of its geographical adaptation may acquire a more meaningful solution if it is considered in terms of the ecological genetics of the species

(Lerner, 1964), which has three major levels: genetic (Mayr, 1954), somatic (Williams, 1957) and ecological (Andrewartha and Birch, 1954).

Body weights, developmental times and productivity traits of twelve populations, derived from widely separated localities throughout the distribution of the species, were studied. All of the populations were obtained from different research laboratories and some are being used for genetical and ecological studies. Using appropriate statistical techniques geographical variation in such species may be demonstrable.

LITERATURE REVIEW

One of the major influences in the variation of species has been the geographic variation of the environment. Evidence for the adaptive nature of insects to geographic variation had come from: geographic variation of physiological characters, ecogeographic rules and geographic variation of balanced polymorphism. The two biological phenomena in the present investigation, population differentiation and clinal variation, were studied regarding their biological significance in terms of natural selection. These phenomena are two of the classification of geographic variation proposed by Hubbell(1956).

I. Population Differentiation:

Variation occurs within and between local populations of the same species. Although records of such differences among spatially separated populations of a species, called geographic variation, have been found earlier than the Linnaean period (for review see Mayr, 1966), major interest in the study of geographic variation only began during the middle part of the 19th century. Early studies involved physiological differences among different populations of the same species, but it is only within the last few decades that their genetic basis has been determined. Outstanding in this field is the work of Gordon (1947) on fishes and of Dice and his school on mice (Blair, 1950).

Among the earliest outstanding studies of geographical variation in insects was that of Goldschmidt(1934) who studied strains of Lymantria dispar, the gypsy moth, from localities in Europe, Asia, and North America. As the adults were reared under uniform laboratory conditions it was possible to attribute the

observed variability to strain differences in genotype.

A study on a species more closely related to the flour beetles was made by Soderstrom and Wilbur (1965, 1966) who used two geographical populations of Sitophilus oryzae (L.), small weevils from Louisiana and intermediate-sized weevils from Kansas, and a third population of large weevils S. zeamais (Mot.). Significant differences in size, reproductive potential and developmental time were noted between the three weevil populations in almost every culture medium tested.

Although studies on geographic variation in T. castaneum have not been reported, review of some genetic studies in T. castaneum may contribute toward clarification of its geographical variation.

Bell and Moore (1958), McNary and Bell (1962), Bray et al. (1962) and Enfield et al. (1965) have demonstrated that pupal body weight of T. castaneum is under genetic control. Blair et al. (1961) and Hardin and Bell (1967) have shown that larval body weight is also under genetic control. Sokoloff (1966b) reported mutant genes for T. castaneum which reduce the size of the beetle without deforming it. When these small beetles were mated inter se, the distribution of the resulting adults indicated a large number of factors controlling body size. Bray et al. (1962) obtained symmetrical response in both directions for pupal weight indicating the presence of a large number of genes controlling body size.

Park et al. (1961) demonstrated that genetic differences existed between strains of T. castaneum for various characteristics of their life cycles, such as developmental time of egg, larval and pupal stages. An extensive literature review on the genetics of

developmental rate was made by Dawson (1964b) who reported that developmental rate in T. castaneum is under genetic control.

Developmental rate in T. castaneum is an important component of fitness (Dawson, 1965a). Artificial selection for extreme developmental rates (fast and slow) lead to a reduction of such fitness. Analysis of developmental rates of inbred lines and their hybrids (Dawson, 1964b) showed that other than evidence of maternal effect in some crosses all hybrids showed heterosis for fast development. Also a number of lethal and semi-lethal genes affect the developmental process (Dawson, 1964c).

Environmental factors such as temperature, humidity, type and condition of food also have an effect on developmental rate (see for example, Park and Frank, 1948; Gray, 1948; Howe, 1956; and Karten, 1965).

It is evident that growth during larval and pupal stages is under genetic control. Snodgrass (1954) pointed out that metamorphosis has its roots in the course of embryonic development. The individual organs and tissues probably have their specific instructions mainly from genetic and earlier epigenetic sources (Wigglesworth, 1959). Needham (1964) stated "In the genome is the codification of the entire intrinsic mechanism of control determining the whole pattern of growth". Williams (1961) indicated that larvae and adults of higher insects seem to have little in common except for their genes. He emphasized metamorphosis at the level of individual cells where there is a coordinated and controlled interplay between nuclear information and cytoplasm. In T. castaneum, Englert and Bell (1963)

compared the entire growth cycle, as measured by body weight, for two inbred lines and their reciprocal hybrids and found genetic differences between the lines.

Productivity of Tribolium strains (mutant or otherwise) is a character subject to variation arising from genetic differences among strains, differences among environments, and differences in the response of the strains to different environments. However the role of genetic differences in determining productivity in flour beetles has received little attention. Studies of productivity of non-mutant strains of T. castaneum have been reported by Lloyd (1957), who compared two laboratory strains (Chicago and Brazil) and by Park, et al., (1961) who found strain differences for natality, mortality, developmental rate, and longevity in strains derived from laboratory stocks having high, intermediate and low productivity. Recently Crenshaw and Lerner (1964) and Sokoloff et al., (1965) have shown that productivity of T. castaneum is under genetic control.

Comparison of productivity of mutant and wild-type strains has been made by Park and Davis (1945), Park (1937), Kollros (1944), and Sokoloff et al. (1965). In general, the findings indicated that homozygote mutants are less productive than heterozygote and wild type. Sokoloff et al. (1965) found that differences in productivity between strains and interaction between strains and environmental conditions were highly significant.

Environmental factors such as type and condition of food, temperature, and humidity have been reported to be limiting factors for the reproductive performance of T. castaneum (e.g., Park, 1954;

Sonleiter, 1961; Howe, 1962; Karten, 1965; and Sokoloff, 1966a, b).

Studies on genetic and phenotypic variations under natural conditions are very limited. Most of the knowledge about the intra-population genetic variations that are associated with phenotypic variation has come from animal breeding experiments. Although Lerner (1955) found a large amount of genetic variation in natural populations having a relatively low phenotypic variation, many evolutionists assume that as a population responds to directional selection pressure, its genetic and phenotypic variation decreases. Simpson (1953a) and Bader (1955) presented evidence supporting a reduction of phenotypic variation in evolving populations. On the other hand Guthrie (1965) reported that the variation is maintained and usually increased. In T. castaneum Dawson (1964b) found all inbred line hybrids showed a reduction in variability for developmental time.

II. Relationship Between Traits:

Very few studies on phenotypic correlations between different components of growth and development in Tribolium have been done. Englert and Bell (1963) examined the relationship of various growth traits of two inbred lines of T. castaneum and their reciprocal hybrids under two environmental conditions. Correlated response for body weight or developmental time during artificial selection for either of them has been investigated by Hardin (1962), Yamada (1963), Englert (1964) and Dawson (1966). The results indicated that a negative change in one of the two traits was associated with selection for the other. Selection for developmental time resulted in a decline in reproductive fitness of most of the selected lines, Englert (1964) and Dawson (1966).

III. Geographical Clines:

In nature, quantitative characters such as body weight, development and productivity are generally correlated with geographical changes of latitude, temperature and humidity. As studies of geographical variation associated with environmental gradients have not been made in Tribolium, studies which had been made in other insects will be briefly reviewed in order to illustrate and clarify the problem. Goldschmidt (1934) studied the gypsy moth, Lymantria dispar under uniform laboratory conditions. He found geographical clines in Japan and Korea in regard to: rate of growth, "strength" of the sex genes, chromosome size, incubation period of the eggs, and degree of larval pigmentation. The clines generally agreed with the climatic changes from northern to southern Japan. Hovaniz (1942) found the butterfly Melitaea chalcidona pupae from coastal southern California larger and heavier than those from Mojave Desert. The change in the pupal characters was parallel with the changes in the climatic conditions. For beetles Rensch (1943) found in two species of Carabus that the subspecies from the subtropical Mediterranean have a smaller size than the races of temperate central Europe. Similar regularities in geographic variation were described by Petersen (1947, 1952) in his studies of Fenno-scandian butterflies. Climatic races have been also reported for Drosophila funebris by Timoféeff-Ressovsky (1935), and for the corn borer Pyraus nubilalis and of the spruce sawfly Gilpinia polytoma by Andrewartha and Birch (1954).

Biometric analyses often aid in the interpretation of geographic variation (Götz, 1959). Alpatov (1929) in his biometrical study of geographical variation in the honey bee in Asia and North

America, found that in Asiatic populations absolute body size, relative size of wax-gland surface, color of abdomen, length of tongue and relative length of legs show clear north south clines on the Russian plains. These clines tend to be reversed in the Caucasus for the first three characteristics. Colonies transplanted to different parts of North America retained their morphological identity under the new environmental conditions, and hence Alpatov concluded that the differences he had observed were genetic, rather than directly due to the environment. Biometric analyses have indicated geographical variation even in the morphologically notoriously uniform genus Drosophila (e.g., Stalker and Carson, 1947; Prevosti, 1955; and Teissier, 1957). Recently, Sokoloff (1965, 1966a) reported geographic variation of various body characters in D. pseudoobscura derived from a number of localities throughout the distribution range of the species, some as close as six miles and other as distant as 2000 miles. His results indicated that natural populations are genetically distinct not only with regard to chromosomal arrangements, but also with regard to genes controlling the size of body characters.

In the genus Drosophila Timoféeff-Ressovsky (1935) measured the relative viability of different strains of D. funebris from Europe and Russia, and found that strains from southern localities have a relatively high viability at high temperatures, and a lowered viability at low temperatures while the strains from northern localities show just the reverse relationship. Dobzhansky (1935) demonstrated a similar relationship between climate of origin and physiology in the two closely related species D. pseudoobscura and D.

persimilis; in this case the physiological character studied was fecundity at various temperatures.

Ecological rules have been developed to show the adaptation of geographic populations to their environmental conditions. One example, Bergmann's rule, expresses the relationship between body size and environmental condition, where the smaller-sized geographic populations of a species are found in the warmer part of the range and the larger-sized races in the cooler ones (Mayr, 1942, 1966 and Ray, 1960). On the other hand Scholander (1955) agreed that Bergmann's rule could apply to poikilotherms and homoiotherms if the rule is defined as a simple observation made intra-specifically and correlating size with temperature. He doubted its significance in terms of heat conservation.

Clines for increased size correlated with lower environmental temperature had been found in many poikilotherms such as Drosophila and other species (Alpatov and Pearl, 1929; Eigenbrodt, 1930; Imai, 1937; Gunn, 1942; Stalker and Carson, 1947; Bullock, 1955; Ray, 1960; and Tantawy and Mallah, 1961). The inverse of Bergmann's rule has also been reported in poikilothermal animals (Park, 1949 and Hesse et al., 1951).

Geographic variation has been found in every adequately studied case of polymorphism (see for example reviews by Mayr, 1942, 1951; Ford, 1945; Huxley, 1955; Voipio, 1950; and Andrewartha and Birch, 1954). Some of the more detailed studies of geographic variation of polymorphism in insects are bumblebees Bombus (Reinig, 1939), the lady beetle Harmonia oxyridis (Dobzhansky, 1933; Komai et al.,

1951), and Drosophila (Dobzhansky, 1951; Patterson and Stone, 1952). Some species showed a rather even degree of polymorphism throughout their ranges, while others are highly polymorphic in some areas and rather uniform in others. Among the rather even polymorphic species are, for instance, Drosophila willistoni (Dobzhansky, 1957) and D. subobscura (Stumm-Zollinger and Goldschmidt, 1959). Gene arrangements of D. willistoni that were most common in southern Brazil were also most common in Cuba and Florida (Townsend, 1952; and Dobzhansky, 1957).

IV. Evolution, Distribution and Life History of *Tribolium castaneum*:

The origin of Tribolium has been difficult to determine because their distribution by commerce has made them quite cosmopolitan. Good (1936) suggested that flour beetles originated somewhere in the general region comprising India, Southwest Asia, and Eastern Mediterranean countries. Blair (1930) has shown that T. castaneum exists in wild stage in India. Samples of Tribolium, not known whether confusum or castaneum were found in a jar removed from an Egyptian tomb which had probably contained grains of wheat.

On the basis of morphological resemblance and geographic distribution of the various species-groups, Hinton (1948) suggested that the genus Tribolium must have originated from a common ancestor in the late Cretaceous or possibly earlier (Figure 1).

Even though T. castaneum occurs throughout the world (Figure 2), its geographic distribution suggests that it is less frequent in colder climates. Although T. confusum can stand colder climates than T. castaneum the failure of world distribution maps to show any difference in the northerly distribution of the two

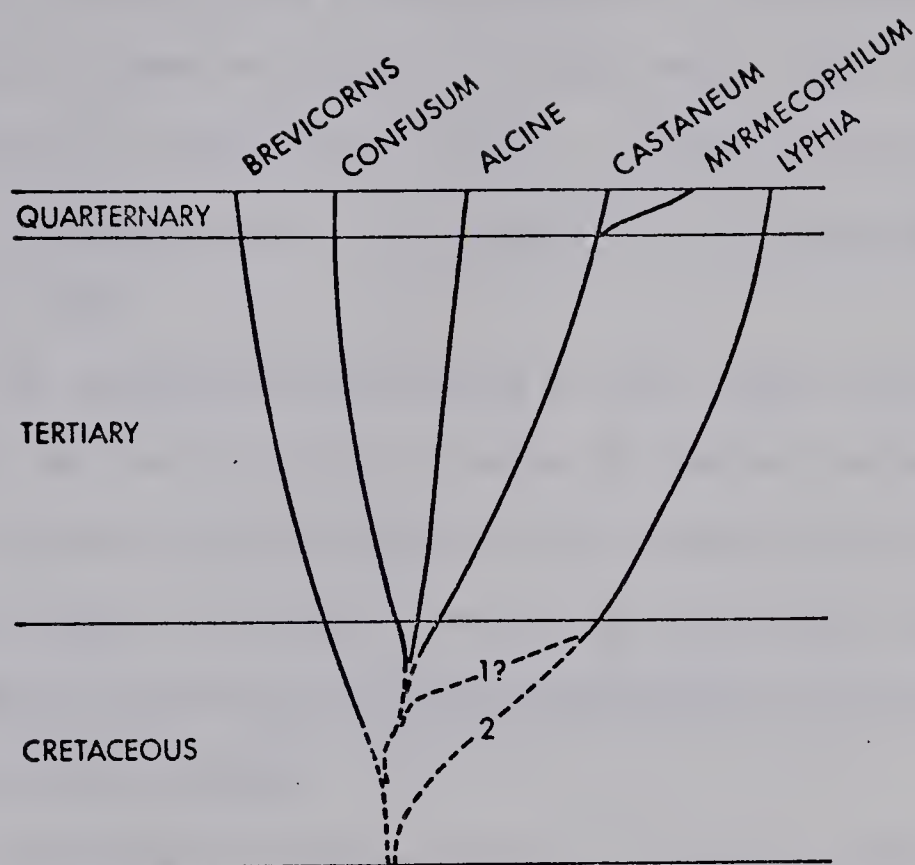


Figure 1. Phylogeny of *Tribolium* species (after Hinton, 1948).



Figure 2. World distribution of *T. castaneum* (modified after Good, 1936).

species may be due to both species having been introduced and established in heated buildings in climates much colder than they could ordinarily tolerate (Good, 1936). In areas closer to the equator T. castaneum becomes more common than T. confusum (Sokoloff and Lerner, 1967).

The castaneum species group is very viable (evolutionary plasticity) and has split into a number of distinct secondary species-groups. The major differentiation of the species occurs between the present Asiatic mainland region and the Australian region, where there has been isolation of Tribolium populations on different kinds of islands (Hinton, 1948).

Although the original habitat of Tribolium appears to have been in rotting logs and under bark (Good, 1936); whole wheat grain, flour and other wheat products now comprise the most important sources of food. However, the insect does feed on a large variety of other materials such as grain (rarely found in maize), corn flour, starchy materials, beans, peas, ginger, dried plant roots, dried fruits, insect collections, nuts, chocolate, drugs, snuff, cayenne, and pepper.

The adult beetles are very active, moving rapidly when disturbed and may fly occasionally. It appears unlikely that an infestation could spread in this manner, although the flight may be aided by wind. They may survive moderately cold winters in unheated buildings and often live two years or more in the adult stage, during which the female may produce up to 1,000 eggs. The very small clear-white sticky eggs hatch in five to seventeen days into small

brownish-white larvae, becoming full-grown in one to four months depending upon temperature, humidity and kind of food, and are then about $1/6$ inch in length. They change to white naked pupae, remaining in this stage for one to two weeks after which they emerge into adults. All stages of the insect (Figure 3) may be found at anytime of the year (Good, 1936).

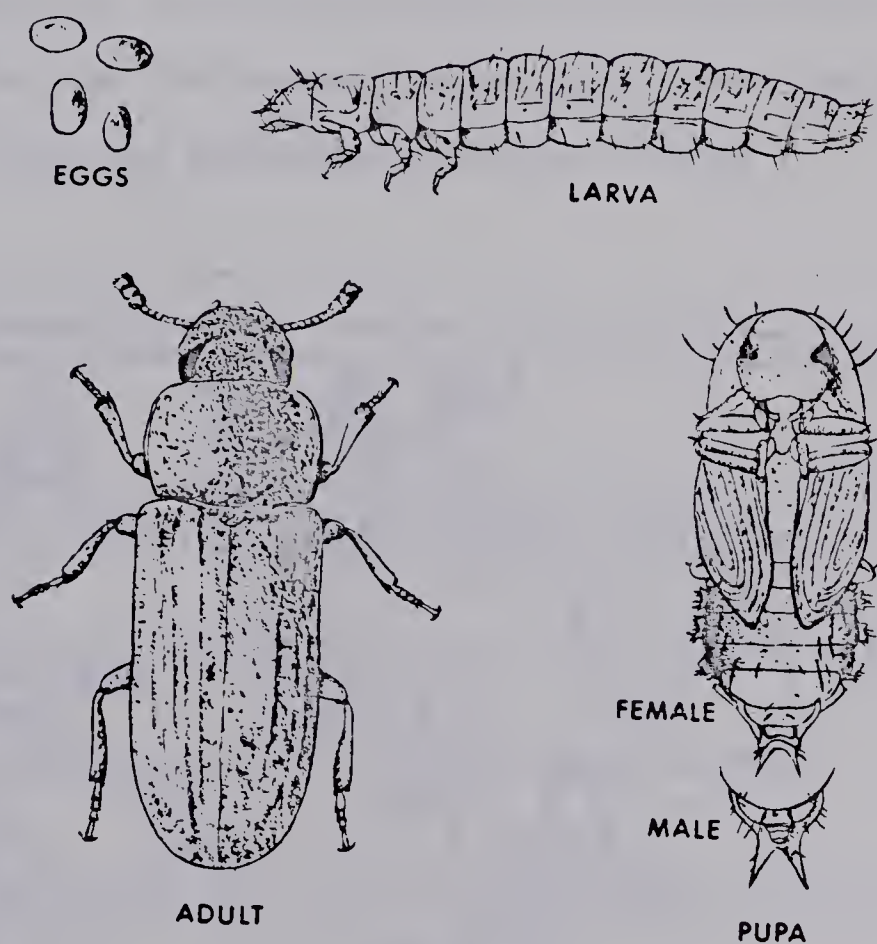


Figure 3. Different stages of T. castaneum life cycle.

MATERIAL AND METHODS

a. Populations:

Samples of twelve populations of Tribolium castaneum were obtained from research laboratories located in Europe and North America (Table 1, Appendix). The sample size obtained from these laboratories was more than 100 for most populations. Locations from which the populations were originally collected are shown in Figure 4. The code names which hereafter will be used to refer to the populations, location of original collection, and available information from the research laboratories concerning the origin and past culturing techniques are given in Table 1.

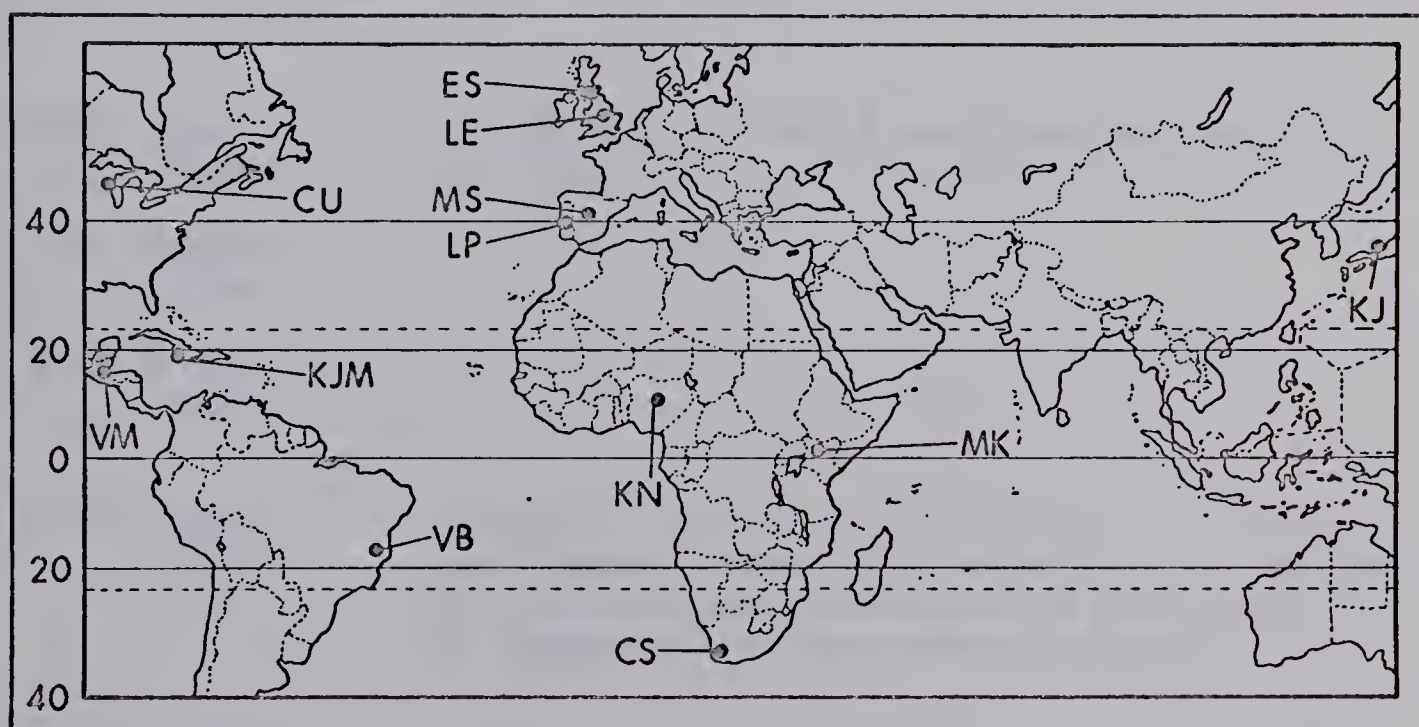


Figure 4. Geographic locations from which the twelve populations of T. castaneum were originally collected. (For explanation of symbols see Table 1).

Table 1. Identification code, location of original collection and history of the twelve populations of Tribolium castaneum.

Code	Location of original collection	History
1.CU	Chicago, United States	Collected from a small stock culture obtained from USDA in 1934. Reared at 29°C, 60-75% R.H. in standard media in quart-size jars with bolting-cloth top.
2.CS	Capetown, South Africa	Populations 2, 3 and 4: Mass transfers of about 100 adults per population into 100 grams of standard media at 33°C and 70% R.H.
3.KJ	Kyoto, Japan	
4.VB	Vicosa, Brazil	
5.ES	Edinburgh, Scotland	Reared since 1960 under 25°C and 75% R.H.
6.KN	Kano, Nigeria	Populations 6, 7 and 8 have been kept at 26.5°C and 60% R.H.
7.MK	Makakos, Kenya	
8.KJM	Kingston, Jamaica	
9.LE	London, England	Probably collected after 1942 from an infestation near London. Since 1950, reared at 25°C and 70% R.H. in whole meal flour with 5% dried yeast in 6" diameter glass jars with gauze tops.
10.LP	Lisbon, Portugal	Reared since 1957 in whole wheat meal at 25°C and 70% R.H. Adults (100) were left for 4 weeks for egg laying, in 1/2 litre container, and then discarded. New adults were removed after 2 weeks, after which weekly sievings were made to obtain insects for new cultures. The new cultures were kept in production for about 10 weeks.

11. MS Madrid,
Spain
- In July, 1964, a sample of 1,000 individuals was obtained from a pool of several collections of wild populations. A criss-cross transfer every 2-3 months was made. From each of 5 bottles 25-30 individuals (larvae or pupae) were removed and mixed with individuals of the other four bottles, therefore 125-150 individuals in each of five bottles were used to maintain the population in standard media at 33°C and 70% R.H.
12. VM Veracruz,
Mexico
- Collected from white corn flour. Maintained at room temperature (25°C) in wheat. In summer 30 adults and in winter 40 adults were used to produce the next generation.
-

b. Traits measured:

Body weight, developmental time and productivity trait parameters were measured for each population as described in Table 2.

Productivity of T. castaneum has been defined in different ways. Sokoloff and Ho (1962) and Sokoloff et al. (1966a, b) defined productivity as "the number of adult progeny produced per given number of females in a given interval". Sokoloff et al. (1965) defined it as "number of adult progeny per female parent per day of parental confinement". Crenshaw and Lerner (1964) defined it as "the number of offspring still living approximately one month after removal of parents from a vial containing excess of food resources". In this investigation, productivity was measured as indicated in Table 2 for the same females measured for body weights.

Table 2. Identification code and description of traits measured for each population.

	Code	Trait	Description
Body weight (10^{-5} gm.)	Lw	Larval weight	Individual 13-day larval weight, measured after 24 hours egg laying.
	Pw	Pupal weight	Weight on day of pupation.
	Aw	Adult weight	Weight on day of adult emergence.
Developmental time (days)	Pt	Pupation time	From first day egg to first day pupa..
	At	Adult emergence time	From first day egg to first day adult emergence.
	Dp	Duration of pupal stage	Duration between first day pupation to first day adult emergence.
Productivity	Pp	Period of Productivity	Number of 10-day intervals in which offspring observed after mating at 27 days of age. Counting stopped at first period having zero offspring or maximum of 20 periods.
	Tp	Total Productivity	Total number of offspring (all stages) counted during the periods of productivity.

c. Culturing and experimental techniques:

Because T. castaneum developmental rate is dependent on temperature and humidity (Howe, 1956), the populations were reared in a modified chick incubator operated at a controlled temperature ($33\pm.5^{\circ}\text{C}$) and humidity ($70\pm 2\%$ R.H.) in the laboratory at the University of Alberta. Prior to the beginning of the experiment the populations were mass mated for two generations to minimize the

possible maternal effect suspected by Dawson (1964a) in T. castaneum. Each generation, approximately 25 males and 25 females (pupal stage) were mass mated in a box containing 25 grams of standard media (95% whole wheat flour and 5% dried brewer's yeast). Media from the same batch were used to reduce uncontrollable environmental differences. The experimental procedure for estimating population parameters for growth traits are given in Table 3 and for productivity in Table 4.

Table 3. Experimental procedures for measuring growth traits.

Day	Procedure
0	Fifty unsexed adults from each population were placed in a clean plastic box containing media for 24-hour egg collection.
1	Twenty-four hours after being placed in the box, the adult beetles were removed from media.
13	Thirty 13-day old larvae were individually weighed from each population and placed into identifiable individual 3/4 oz. coffee creamers containing one gram standard media.
17-on	On day of pupation, pupae were sexed, weighed and returned to creamer.
20-on	On day of emergence, adults were weighed and returned to creamer.

Table 4. Experimental procedures for measuring productivity.

Day	Procedure
27	Matings of one male and one female were made. Number of matings equal to the number of the sex with fewer individuals. Extra individuals of opposite sex were discarded.
37	Adult pairs transferred to new creamer to start second period.
47	a. Adult pairs were transferred to new creamer to start third period. b. Count of offspring (all stages) of first period of productivity. Count was continued from 47 to 52-day.
57	a. Adult pairs were transferred to new creamer. b. Count of offspring (all stages) of second period of productivity. Count was continued from 57 to 62-day.
Transfer was made every ten days until a maximum of 20 periods or until productivity ceased, whichever came first.	

Although indicated in Table 4 that matings were made on day 27, in some populations, e.g. K.J., some larvae took more than 27 days to develop to adults and therefore matings were made whenever a pair of male and female adults were available.

d. Statistical techniques:

Five replicates were planned for each population. However due to differences in productivity of the base populations which resulted in insufficient number of 13-day old larvae this was not possible for all populations. LE and LP populations were replicated four times, MS population twice, and MK population only once.

To determine whether there were significant differences among populations, an analysis of variance was computed for each of the eight traits studied. The model used was:

$$Y_{ijk} = u + P_i + S_j + PS_{ij} + R_k + RP_{ik} + RS_{jk} + PSR_{ijk}$$

where the usual analysis of variance assumptions were made and where:

Y_{ijk} is the mean value for the i^{th} population of the j^{th} sex in the k^{th} replicate.

u is the overall mean.

P_i is the fixed effect of the i^{th} population.

S_j is the fixed effect of the j^{th} sex.

PS_{ij} is the interaction of the i^{th} population with the j^{th} sex.

R_k is the random effect of the k^{th} replicate.

RP_{ik} is the interaction of the k^{th} replicate with the i^{th} population.

RS_{jk} is the interaction of the k^{th} replicate with the j^{th} sex.

PSR_{ijk} is the interaction of the i^{th} population with the j^{th} sex and the k^{th} replicate.

Only those eight populations which had been replicated five times and are indicated by asterisks in Tables 2, 3, 4 Appendix were used in the analyses. Although each replicate was started with 30

larvae(13-day old), unequal numbers of individuals resulted from mortality. Unweighted means of each population and sex group were computed. These were used in the analyses of variance with the error term calculated from the individual observations and corrected using the harmonic mean (Snedecor, 1967). Duncan's multiple comparisons test (1955) was used to compare each population mean with every other population mean.

Since the absolute variation measured as standard variation does not necessarily reflect the actual intrinsic or relative variation (Lewontin, 1966), the variability was measured as coefficient of variation ($\frac{S}{\bar{X}} \times 100$) for each trait within a given population for both males and females.

Correlations and regression were used to determine relationships between variables in the different populations for both sexes.

RESULTS

I. Population DifferencesA. Body weights:

The means for larval, pupal, and adult weights of males and females in each of the twelve populations are given in Table 2 (Appendix) and presented graphically in Figure 5 according to latitude. Results of the analyses of variance of the means for the eight populations which had five replicates are given in Table 5.

Table 5: Analyses of variance of body weights of eight populations.

Source of variation	d.f.	Mean square		
		Larval weight	Pupal weight	Adult weight
Population (P)	7	3841.0*	6271.1*	3939.0*
Sex (S)	1	.9	4391.4*	4124.6*
PS	7	17.1	60.5	74.6
Replicate (R)	4	3393.1*	459.4*	951.3*
PR	28	182.8*	132.3*	86.1*
SR	4	41.5	29.4	55.0
PSR	28	27.6	62.3	67.2
Error (Corrected)	(a)	89.3	74.0	55.2

* significant at the .05 level of probability.

(a) error d.f. = 1118 (larvae), 1085 (pupae) and 1073 (adult).

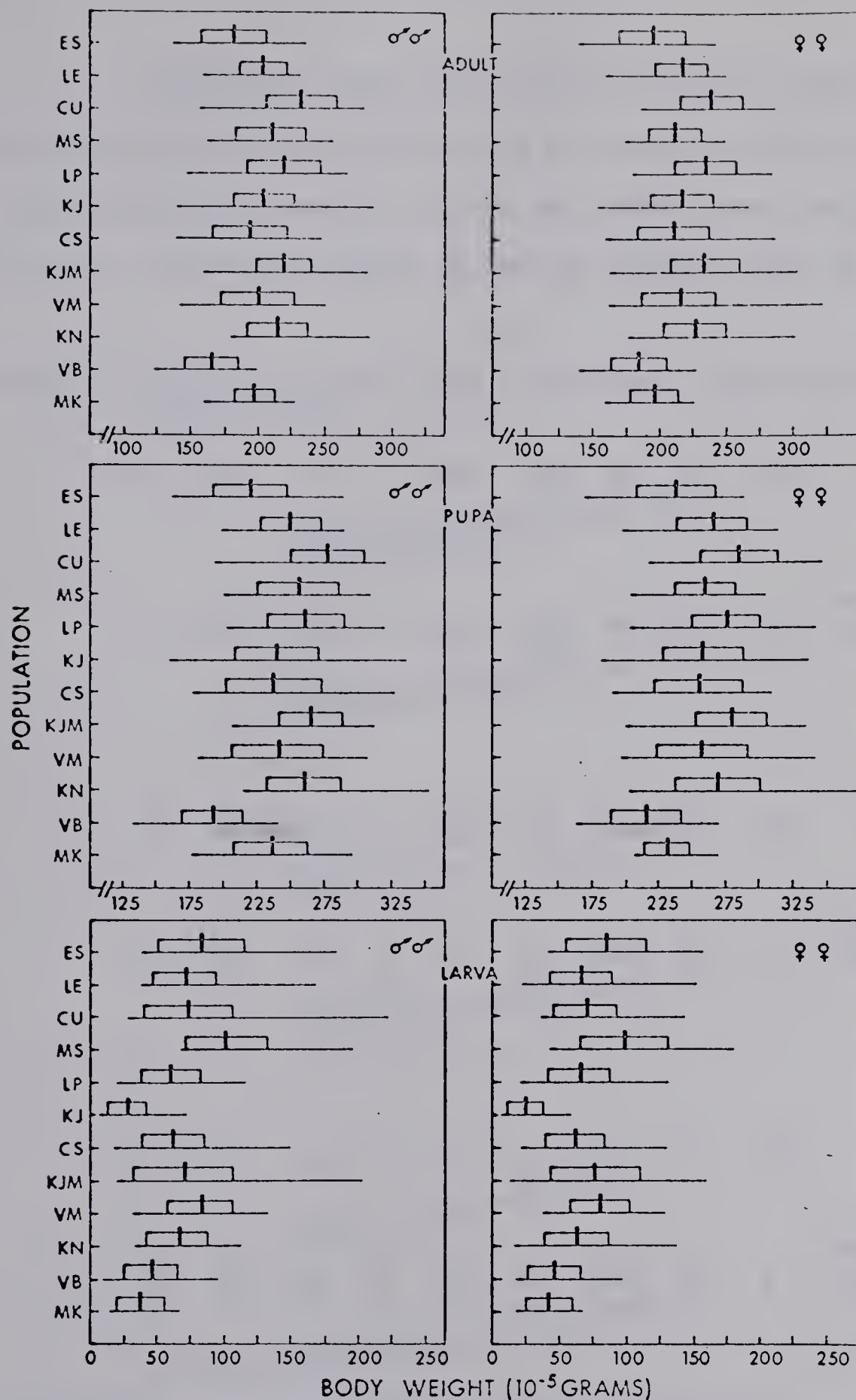


Figure 5. Population means of body weights of the twelve populations of *T. castaneum* (see Table 1 for population identification). For each diagram the horizontal line represents the sample range, the vertical line the mean, and the rectangle the value of standard deviation on each side of the mean.

Differences among populations were highly significant for all traits and were the major source of variation. The results of Duncan's multiple range test of the body weight means are given in Table 6. For larval weights, KJ was the lightest (29.1 for males

Table 6. Duncan's multiple range test of body weight means* (eight populations).

KJ	VB	CS	KN	KJM	CU	VM	ES	♂	
KJ	VB	KN	CS	CU	KJM	VM	ES	♀	Larval weight
VB	ES	CS	VM	KJ	KN	KJM	CU	♂	
VB	ES	CS	VM	KJ	KN	KJM	CU	♀	Pupal weight
VB	ES	CS	VM	KJ	KN	KJM	CU	♂	
VB	ES	CS	VM	KJ	KN	KJM	CU	♀	Adult weight

* Populations underscored by the same line are not significantly different at .05 level of probability.

and 26.4 for females) and ES the heaviest (86.6 for males and 85.3 for females). MS which was not included in the multiple comparison showed even heavier larval weight (101.7 for males and 99.1 for females). VB was the lightest for pupal (193.4 for males and 216.6 for females) and adult weights (166.5 for males and 185.2 for females), while CU was the heaviest for both pupal and adult weights (278.3 for male and 285.0 for female pupal weights; and 233.9 for male and 239.6 for female adult weights). Population differences in body weight measurements will be mentioned again under geographical clines.

Males differed significantly from females for pupal and adult weight, but not for larval weight. These differences were consistent as female pupal and adult weights were heavier than male pupal and adult weights for all populations (Table 2, Appendix). Gray (1948) and Boylan and Wong (1965) also found that female pupal weights were heavier than male pupal weights.

Although conditions were standardized throughout the experiment, replicates were significantly different for larval, pupal and adult weights. Similar differences were observed by Karten (1965). Such replication effect could be due to the experimental design. Each of the five replicates were obtained from the same base population with an interval of 1 - 2 weeks required to collect each replicate. Therefore the progeny of the fifth replicate were from parents up to eight weeks older than the same parents in replicate 1. Consequently age of the parent females at the time of taking the egg samples may account for part of the difference found between replicates as previously noted by Boylan and Wong (1965).

B. Developmental times:

The means of pupation time, duration of pupal stage and adult emergence time of males and females in each of the twelve populations are presented in Table 3 (Appendix) and illustrated for pupation time and adult emergence time in Figure 6 according to

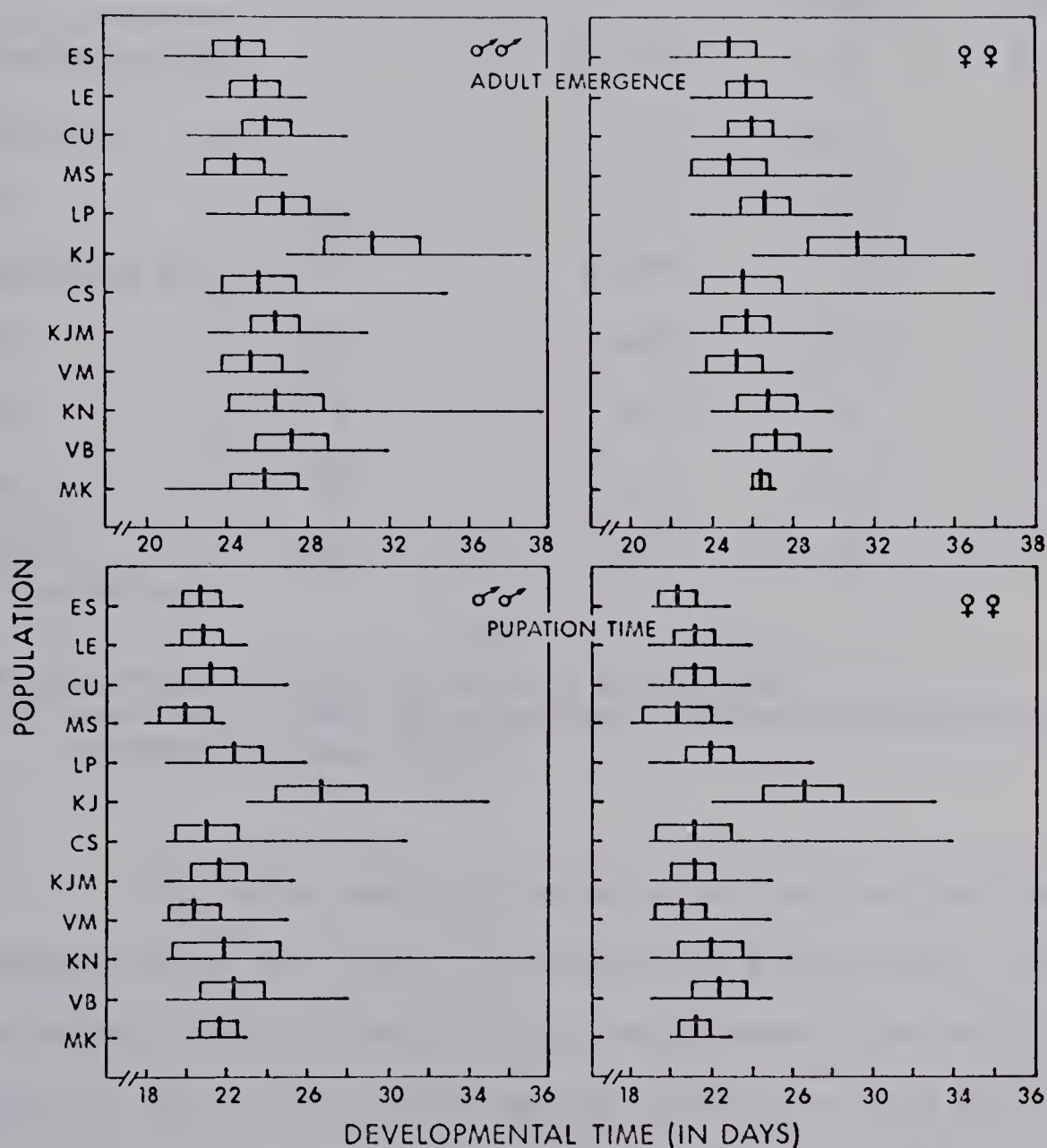


Figure 6. Population means of developmental times of the twelve populations of *T. castaneum* (see Table 1 for population identification and Figure 5 for other descriptions).

latitude. Results of the analyses of variance of the means for the eight populations having five replicates are given in Table 7.

Table 7: Analyses of variance of traits of developmental time of eight populations

Source of variation	d.f.	Mean square		
		Pupation time	Duration of pupal stage	Adult emergence time
Population (P)	7	41.31*	.08	41.77*
Sex (S)	1	.25	.01	.34
PS	7	.03	.01	.36
Replicate (R)	4	6.29*	.12*	6.38*
PR	28	.48*	.05*	.52*
SR	4	.57	.04	.74
PSR	28	.21	.03	.37
Error (Corrected)	(a)	.21	.02	.27

* significant at the .05 level of probability

(a) error d.f. = 1085 (pupation) and 1059 (adult emergence and duration of pupal stage)

The major source of variation for pupation time and adult emergence time was due to differences among populations. The results of Duncan's multiple range test of developmental time are given in Table 8. For both traits ES was the fastest, for both males (20.1 and 24.6 days) and females (20.4 and 25.0 days) and KJ was the slowest, for both males (26.7 and 31.3 days) and females (26.7 and 31.4 days). There was no significant difference among populations for

Table 8: Duncan's multiple-range test of developmental time means* (eight populations).

ES	VM	CS	CU	KJM	KN	VB	KJ	♂	
				_____	_____				
		_____	_____	_____					Pupation time
	_____	_____	_____						

ES	VM	CS	KJM	CU	KN	VB	KJ	♀	
			_____	_____	_____				
		_____	_____	_____					
	_____	_____	_____						

ES	VM	CS	CU	KJM	KN	VB	KJ	♂	
				_____	_____				
		_____	_____	_____					Adult emergence time
	_____	_____	_____						

ES	VM	CS	KJM	CU	KN	VB	KJ	♀	
			_____	_____	_____				
		_____	_____	_____					
	_____	_____	_____						

* Populations underscored by the same line are not significantly different at .05 level of probability.

duration of pupal period which is illustrated in Figure 7 according to latitude. Population differences in developmental time will be mentioned again under geographical clines.

Although sexes were not significantly different for any of the traits, males developed faster than females for all populations except LP and KJM (Figure 6). Gray (1948) found a small difference between the two sexes in the length of development. The significant differences among replicates as observed here, have also been observed for pupal period in T. confusum by Raychaudhuri and Butz (1965) who considered it as due to differences in parental age between replicates

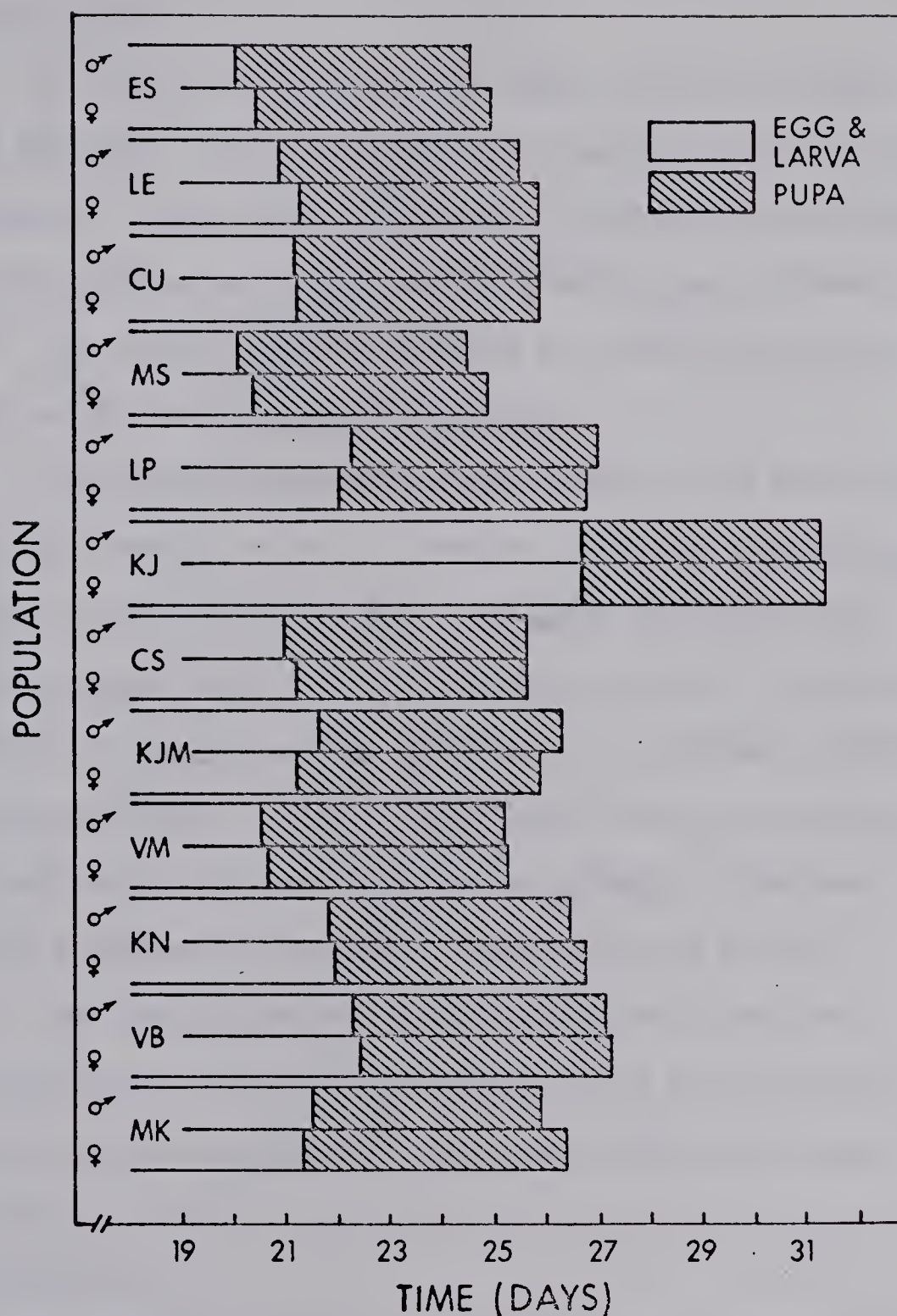


Figure 7. Duration of post embryonic stages of the twelve populations of T. castaneum (See Table 1 for population identification).

and in T. castaneum by Karten (1965) where there was a significant difference for developmental rate between two experimental replicates obtained a week apart.

C. Growth curve:

The means of 13-day larval, pupal and adult weights (Table 2, Appendix) were combined with the means of pupation and adult emergence times (Table 3, Appendix) for the eight populations having five replicates to comprise the growth curves plotted in Figure 8. The 13-day larval weight was at a fixed time but pupal and adult weight varied among individuals.

The general appearance of the curves is in agreement with the experimental curves of Brindley (1930) for T. confusum and Englert and Bell (1963) for T. castaneum, who found that during development larval weight gradually increases, reaching a peak prior to pupation, after which there is a gradual decrease until adult emergence. In this study there was only one measurement in body weight for each stage of development, therefore, the expected exponential nature of the curve could not be detected. The small pupal and adult weights for VB and the large developmental times for KJ separate these two populations from the other populations which still show differences among their growth curves.

D. Productivity.

The means for length of productive period and total productivity in each of the twelve populations are presented in Table 4 (Appendix), and shown graphically in Figure 9 according to latitude. Analyses of variance for both traits are presented in Table 9 for the eight populations having five replicates..

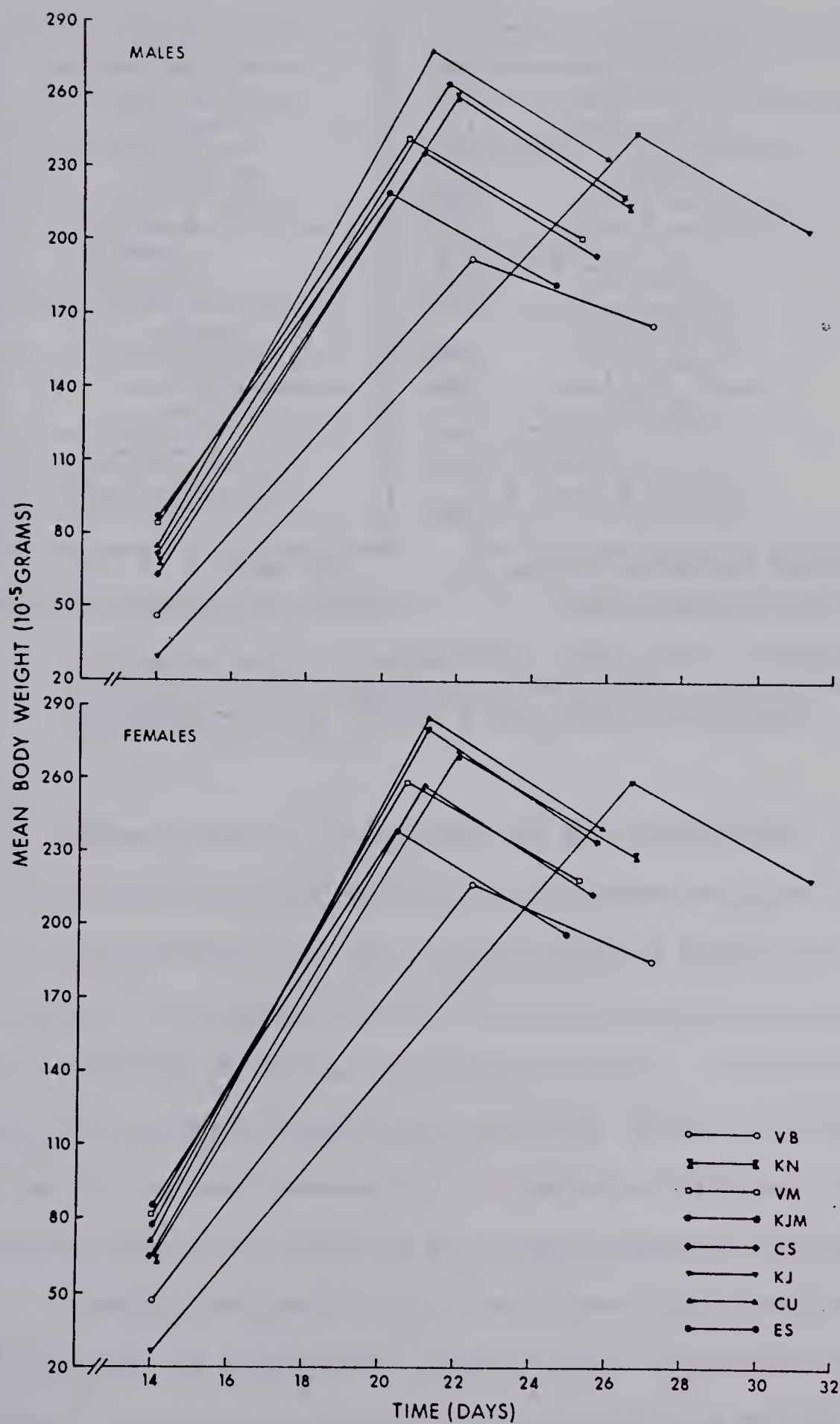


Figure 8. Overall growth curves of eight populations of *T. castaneum* used in the analyses of variance (See Table 1 for population identification).

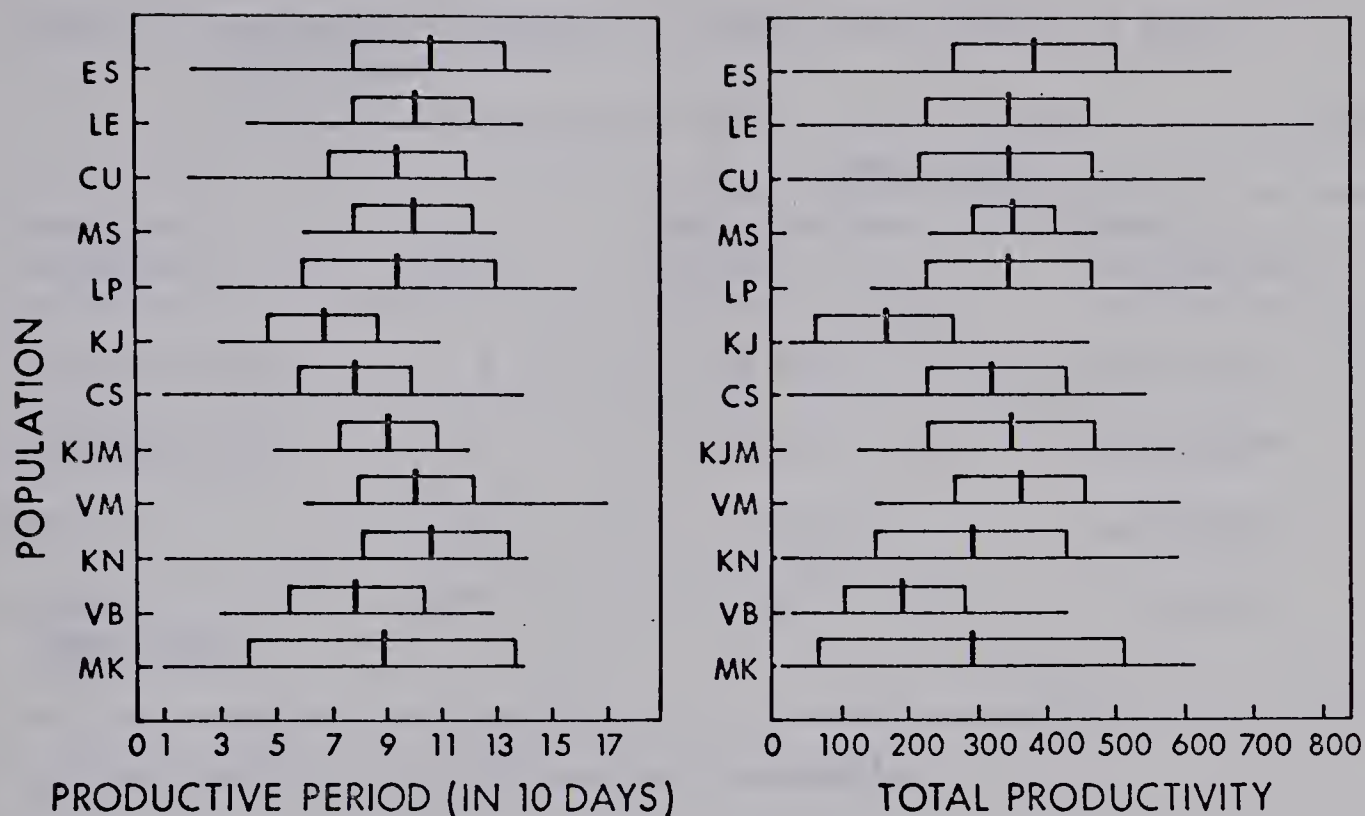


Figure 9. Population means of productivity traits of the twelve populations of *T. castaneum*, (see Table 1 for population identification and Figure 5 for other description).

The major source of variation was among populations. The results of Duncan's multiple range test of the means are given in Table 10. Productivity of KJ was the least (169.5) while ES had the largest (386.8). KJ population also had the shortest period of productivity (6.7) and ES had the longest period (10.7). LP which was not included in the multiple comparison showed even larger productivity (394.2) in 9.4 periods of productivity. Population differences in productivity traits will be mentioned again under geographical clines.

Although the parents in this study were drawn from the same base populations and experimental conditions were controlled, still a significant replication effect was observed for total productivity and not for reproductive period. Bartlett and Bell (1962) also found a

E. Phenotypic variation:

Phenotypic variation expressed as coefficients of variation for body weights, developmental times and productivity traits are given in Table 5 (Appendix) and shown in Figures 10, 11 and 12

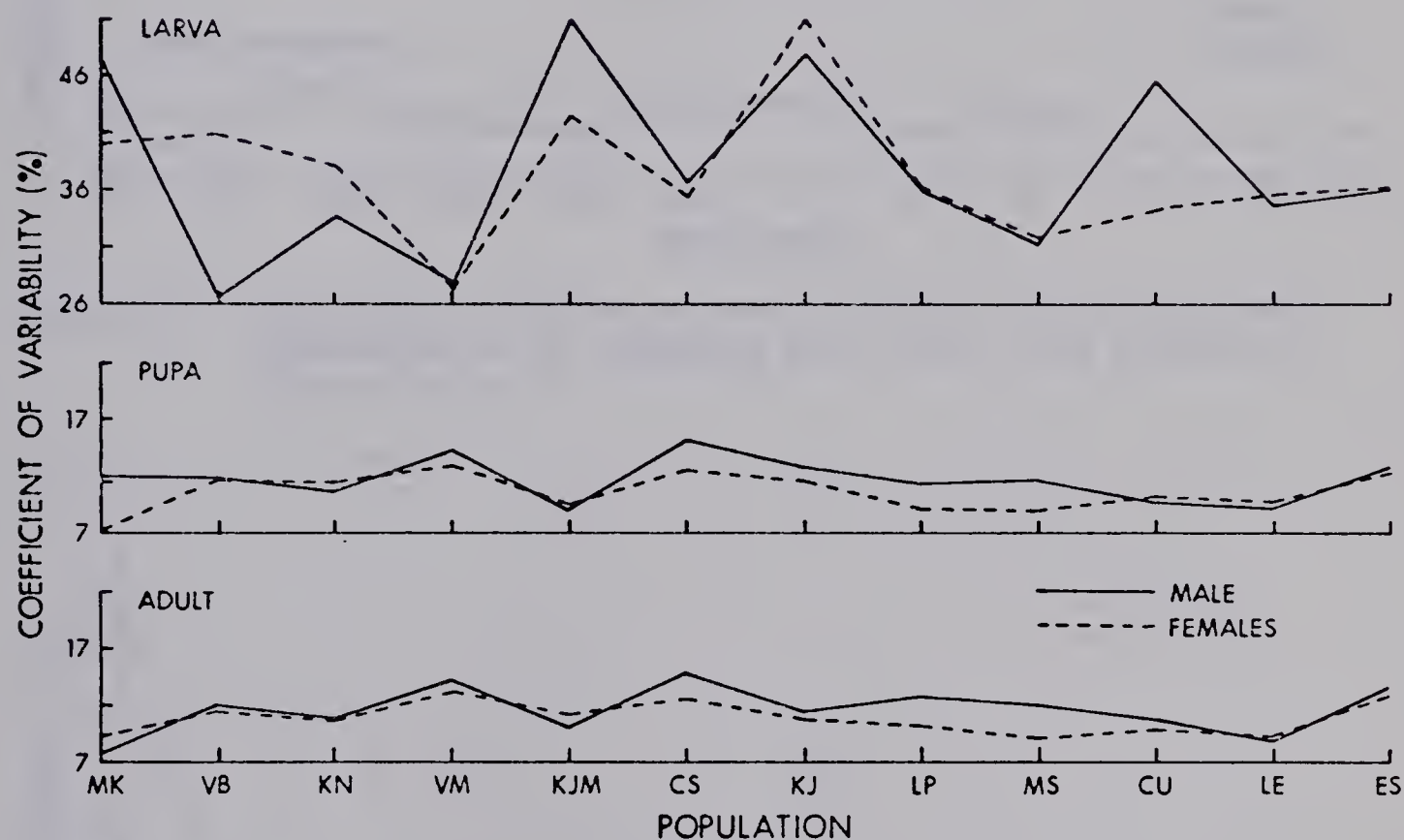


Figure 10. Phenotypic variation of body weights of the twelve populations of *T. castaneum* (see Table 1 for population identification).

according to latitude. Most striking is the large variation within populations for larval weight (Figure 10), period of productivity and total productivity (Figure 12). The summary of coefficients of variability (Table 11) indicates that total productivity had the largest variation within populations (76%) and also the greatest difference between extremes for population means, ranging from 17 to

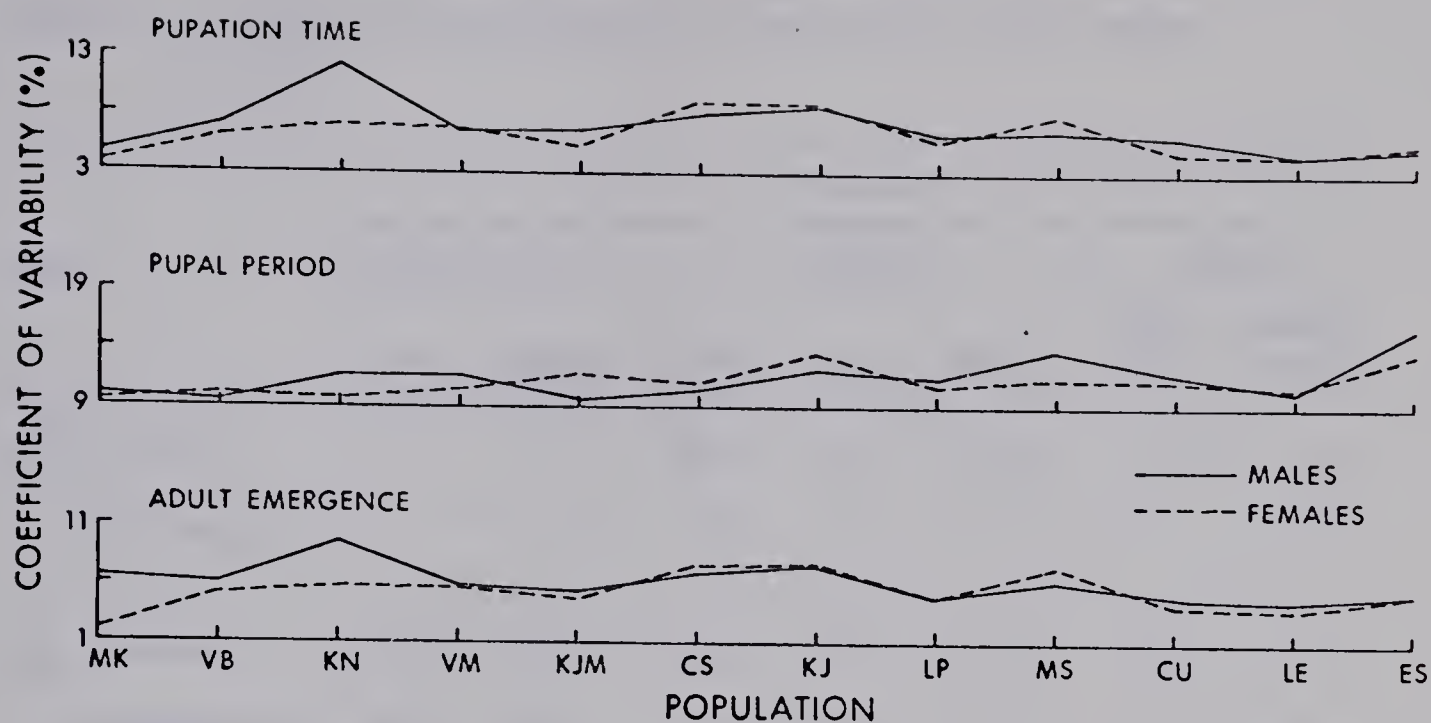


Figure 11. Phenotypic variation of developmental times of the twelve populations of *T. castaneum* (see Table 1 for population identification).

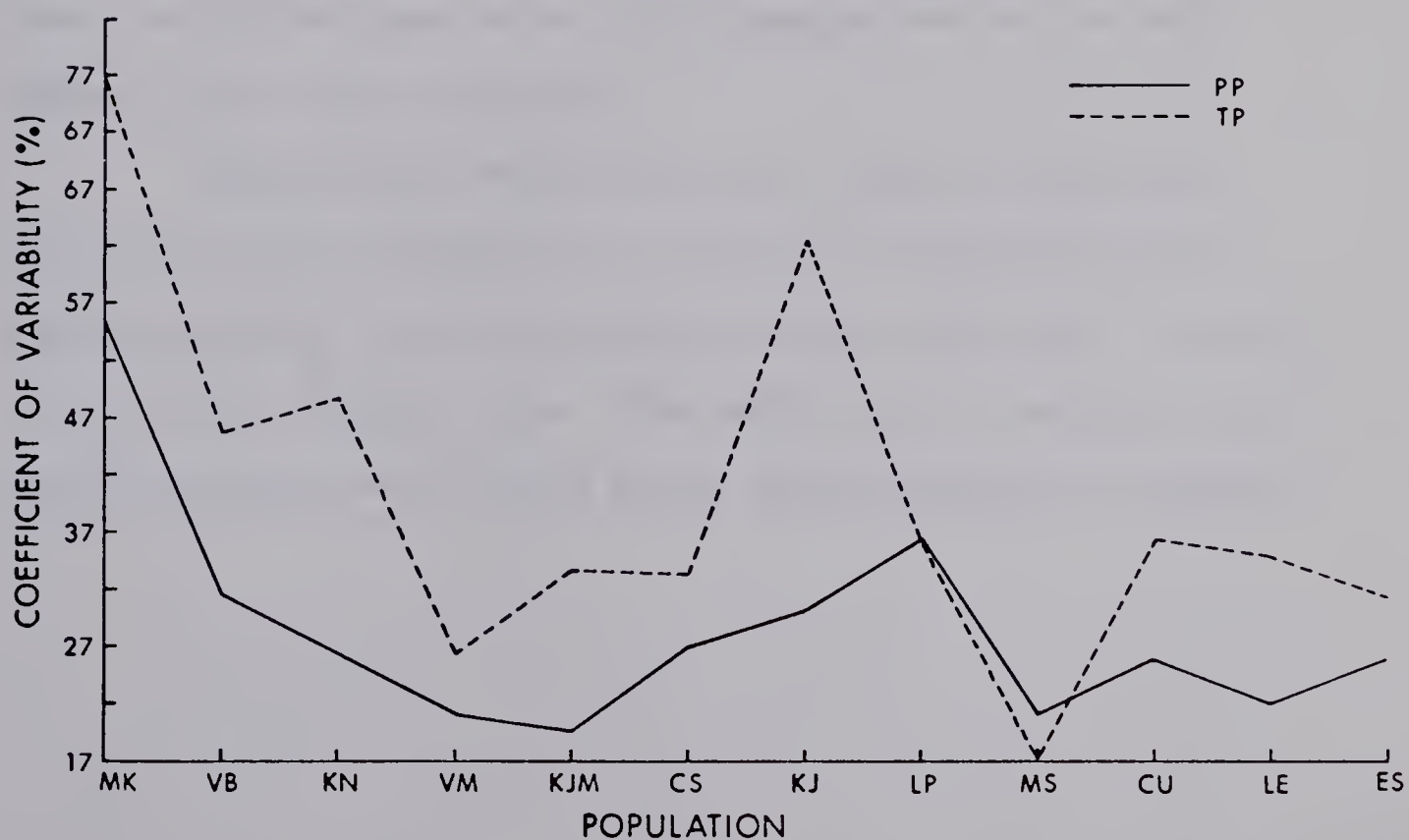


Figure 12. Phenotypic variation of productivity traits of the twelve populations of *T. castaneum* (see Table 1 for population identification).

Table 11: Summary of coefficients of variation of the seven traits.

Sex	Traits						
	Productivity		Weight			Time	
	Total	Period	Larval	Pupal	Adult	Pupa- tion	Adult emerg.
♂♂ min-max	-	-	28-51	9-15	8-15	5-12	5-10
difference	-	-	23	6	7	7	5
♀♀ min-max	17-76	20-60	27-51	7-13	9-13	4-9	2-8
difference	59	40	24	6	4	5	6

76%; period of productivity being next with a range of 20 - 60%.

Larval weight had large values within populations but not such extreme values among populations.

Although body weights were more variable than developmental times within populations, the variation among populations was approximately the same for pupal weight, adult weight, pupation time and adult emergence time. The coefficients of variation of males and females were similar and no distinct pattern was detected.

II. Relationship Between Traits

A. Body weights:

Phenotypic correlation coefficients among the body weight measurements are presented in Table 12. The trait codes referred to in Table 1 will be used in this section. The correlation between larval weight and pupal weight ($r_{LW \times PW}$) or adult weight ($r_{LW \times AW}$) varied considerably among populations, with some populations showing significant negative values and others significant positive values.

In all twelve populations pupal weight was consistently highly correlated with adult weight ($r_{PW \times AW}$) indicating that rankings according to pupal weight would give an accurate ranking of adult weight. A similar relationship was also found by Englert and Bell (1963), who found that the relationship between the two traits was affected very little by environmental or genetical differences. The regression lines of adult weight on pupal weight (Aw on Pw) for eight populations (Figure 13) indicate a positive relationship between the dependent variable, adult weight, on the independent variable pupal weight. All regression coefficients ($b_{AW \text{ on } PW}$) were significantly different from zero at .05 level of probability (Table 6, Appendix). Test of homogeneity (Table 7, Appendix) indicated that differences in regression coefficients among the eight populations were significant for both males and females, although the regression lines appear to be quite similar, because of the small deviations from regression line (Figure 13).

Table 12: Phenotypic correlation coefficients between body weights (Lw, Pw and Aw)

Population	N	$r_{Lw \times Pw}$	N	$r_{Lw \times Aw}$	$r_{Pw \times Aw}$
Males					
CS	72	-.38*	71	-.29*	.90*
CU	78	.14	77	.10	.88*
ES	70	-.06	68	-.05	.88*
KJ	65	.03	64	.10	.92*
KJM	70	.23	70	.05	.88*
KN	75	.34*	75	.37*	.85*
LE	61	-.15	61	-.14	.84*
LP	50	.44*	49	.44*	.82*
MK	15	.63*	14	.63*	.97*
MS	32	-.16	32	-.16	.93*
VB	70	.00	67	.00	.97*
VM	78	-.10	75	-.10	.94*
Females					
CS	75	-.32*	75	-.31*	.89*
CU	69	.40*	66	.32*	.87*
ES	79	.08	79	.16	.91*
KJ	72	.11	72	.18	.93*
KJM	78	.19	78	.30*	.84*
KN	67	.05	67	.18	.90*
LE	57	.22	57	.17	.89*
LP	67	.12	66	.22	.71*
MK	11	.33	10	.32	.83*
MS	28	-.24	28	-.33	.87*
VB	75	.16	74	.17	.95*
VM	71	-.08	71	-.03	.92*

* Significant from zero at the .05 level of probability.

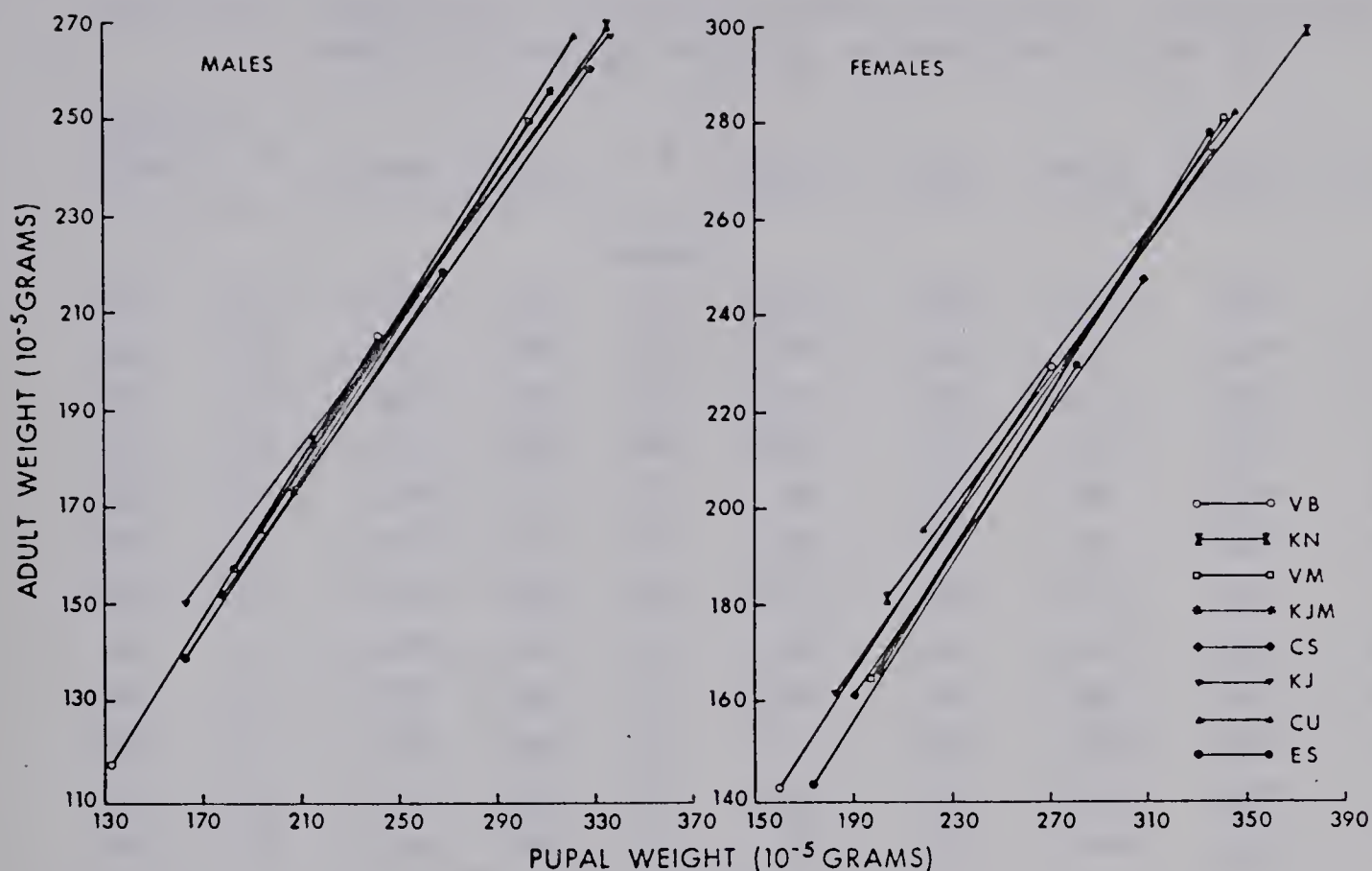


Figure 13. Regression of adult weight on pupal weight of the eight populations of *T. castaneum* used in the analyses of variance (see Table 1 for population identification).

B. Developmental times with body weights:

The phenotypic correlation coefficients of developmental times (Pt and At) with body weights (Lw, Pw and Aw) are presented in Table 13. The significantly negative relationships between larval weight and pupation time ($r_{Lw \times Pt}$) or adult emergence time ($r_{Lw \times At}$) indicate that variation in pupation time or adult emergence time is associated with larval weight in an inverse manner for all populations. The largest larva require less time after thirteen days to pupate or to emerge as an adult.

Similar results were reported by Dawson (1966) who showed that fast developmental times are characterized by decreased length

Table 13: Phenotypic correlation coefficients between developmental traits (Pt and At) and body weights (Lw, Pw and Aw).

Popula- tion	N	r_{LwPt}	r_{PwPt}	N	r_{LwAt}	r_{PwAt}	r_{PtAw}	r_{PtAt}	r_{AwAt}
Males									
CS	72	-.60*	.37*	71	-.67*	.43*	.38*	.96*	.40*
CU	78	-.71*	-.24*	77	-.74*	-.15	-.15	.91*	-.13
ES	70	-.68*	.29*	68	-.68*	.39*	.32*	.85*	.33*
KJ	65	-.65*	.06	64	-.62*	.09	.01	.97*	.04
KJM	70	-.79*	-.17	70	-.79*	-.17	-.08	.95*	-.09
KN	75	-.58*	-.21	75	-.55*	-.23	-.19	.98*	-.24*
LE	61	-.72*	.34*	61	-.71*	.40*	.40*	.92*	.35*
LP	50	-.72*	-.25	49	-.76*	-.18	-.30*	.93*	-.26
MK	15	-.78*	-.75*	14	-.59*	-.40	-.74*	.61*	-.45
MS	32	-.75*	.59*	32	-.77*	.53*	.58*	.92*	.47*
VB	70	-.77*	.33*	67	-.76*	.34*	.33*	.96*	.34*
VM	78	-.63*	.46*	75	-.58*	.52*	.48*	.93*	.48*
Females									
CS	75	-.59*	.23*	75	-.61*	.30*	.27*	.97*	.31*
CU	69	-.71*	-.50*	66	-.70*	-.52*	-.44*	.89*	-.52*
ES	79	-.72*	.19	79	-.73*	.27*	.17	.89*	.20
KJ	72	-.57*	.20	72	-.60*	.19	.11	.97*	.07
KJM	78	-.64*	-.05	78	-.63*	.02	-.08	.90*	-.07
KN	67	-.51*	.12	67	-.55*	.12	.15	.96*	.11
LE	57	-.51*	-.03	57	-.57*	-.14	.02	.88*	-.10
LP	67	-.79*	-.04	66	-.75*	-.04	-.17	.92*	-.17
MK	11	-.76*	-.22	10	-.86*	-.24	.09	.74*	-.34
MS	28	-.52*	.11	28	-.50*	.15	.24	.97*	.25
VB	75	-.66*	.18	74	-.60*	.23	.17	.94*	.19
VM	71	-.64*	.25*	71	-.67*	.27*	.26*	.94*	.22

* significant from zero at the .05 level of probability.

of time spent in all juvenile stages and decreased size. Englert and Bell (1963) found a large negative value for the correlation between larval weight at fifteen days of age and pupation time. Moreover, Hardin (1962) and Yamada (1963) reported a negative change in pupation times during selection for thirteen-day larval weight. Englert (1964) obtained similar results by selecting for early and late pupation times in T. castaneum where pupation time was negatively correlated with 13-day larval weight, values of $-.76$ and $-.86$ being obtained for early and late times, respectively.

The regression lines of pupation time or adult emergence on larval weight (Pt on Lw) and (At on Lw) are given in Figure 14, indicating a negative relation between pupation time or adult emergence and larval weight, as all eight regression coefficients are significantly different from zero (Table 6, Appendix). Tests of homogeneity (Table 7, Appendix) indicate that differences in regression coefficients among the eight populations are significant for both pupation time or adult emergence time on larval weight for both males and females.

The correlation between pupal weight and pupation time ($r_{Pw \times Pt}$) and adult emergence time ($r_{Pw \times At}$) are not consistent among populations, some being significantly different from zero positively, and others significantly different from zero negatively.

The correlation between pupation time and adult emergence time ($r_{Pt \times At}$) is consistently high, in agreement with Dawson (1966). The regression lines (Figure 15) of adult emergence on pupation time (At on Pt) show a positive regression between the dependent variable adult emergence and the independent variable pupation time. Tests of homogeneity (Table 7, Appendix) indicate no significant difference

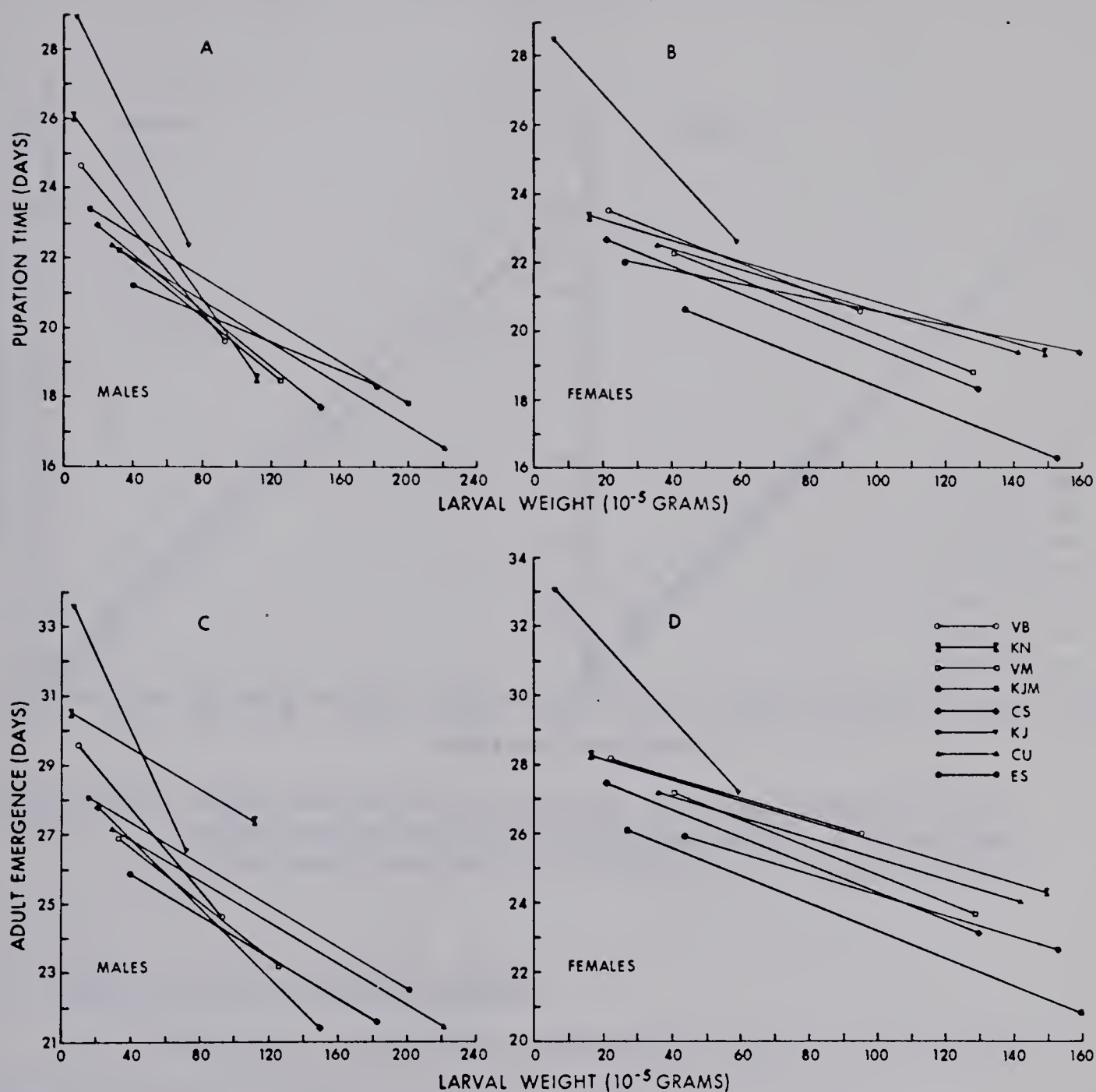


Figure 14. Regression of pupation time (A and B) and adult emergence (C and D) on larval weight of the eight populations of *T. castaneum* used in the analyses of variance (see Table 1 for population identification).

among the regression slopes of different populations for males and females.

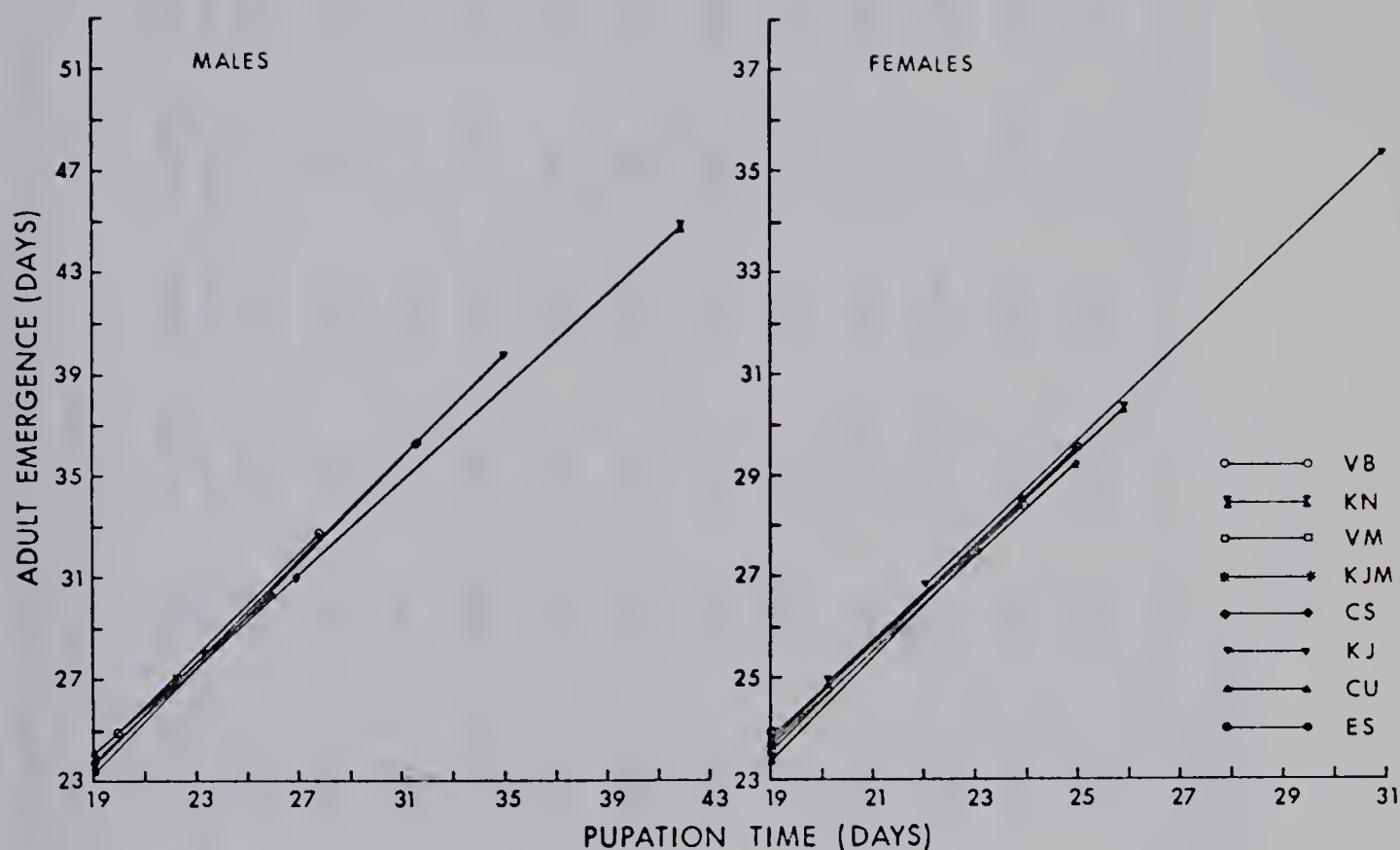


Figure 15. Regression of adult emergence on pupation time of the eight populations of *T. castaneum* used in the analyses of variance (see Table 1 for population identification).

C. Productivity with other traits:

Phenotypic correlation coefficients between productivity traits and other traits are given in Table 14. Only length of productivity (P_p) is closely associated with total productivity (T_p). This is to be expected as the longer a population lays the higher the productivity should be. The positive regressions of productivity on length of productivity (T_p on P_p) are shown in Figure 16. Although there is considerable variation between slopes, the slopes of the different populations do not differ from each other (Table 7, Appendix).

Table 14: Phenotypic correlation coefficients between productivity (Pp and Tp) with body weight (Lw, Pw and Aw), and developmental time (Pt and At) traits.

Popula- tion	N	r_{LwPp}	r_{LwTp}	r_{PwPp}	r_{PwTp}	r_{PtPp}	r_{PtTp}	r_{AwPp}	r_{AwTp}	r_{AtPp}	r_{AtTp}	r_{PpTp}
CS	68	-.10	.08	-.17	-.14	-.06	-.25*	-.23*	-.23	-.09	-.21	.72*
CU	59	-.15	-.02	.09	.14	.16	-.11	.17	.16	.09	-.11	.60*
ES	63	.12	.15	-.06	-.12	.01	-.10	-.01	-.13	-.11	-.14	.59*
KJ	52	.32*	.21	-.02	-.08	-.31*	-.29*	.08	.10	-.31*	-.31*	.53*
KJM	54	.29*	.18	.26	.21	-.11	-.11	.15	.08	-.07	-.06	.39*
KN	57	.14	.21	-.19	-.27	-.02	-.15	-.10	-.20	.01	-.16	.66*
IE	52	.03	-.21	.20	.26	.06	.01	.27	.15	.06	-.01	.37*
LP	39	-.11	-.04	.07	.25	-.01	.07	.00	.11	.10	.19	.78*
MK	10	.26	.22	.73*	.65*	-.24	-.22	.75*	.62	-.37	-.30	.92*
MS	24	.24	.28	-.07	-.33	.27	-.34	-.15	-.47*	.23	-.44*	.22
VB	54	.17	-.06	-.13	.08	-.30*	-.16	-.13	.08	.28*	-.20	.70*
VM	60	-.12	.04	.06	.34*	.14	-.01	-.03	.18	.21	.11	.47*

* significant from zero at the .05 level of probability.

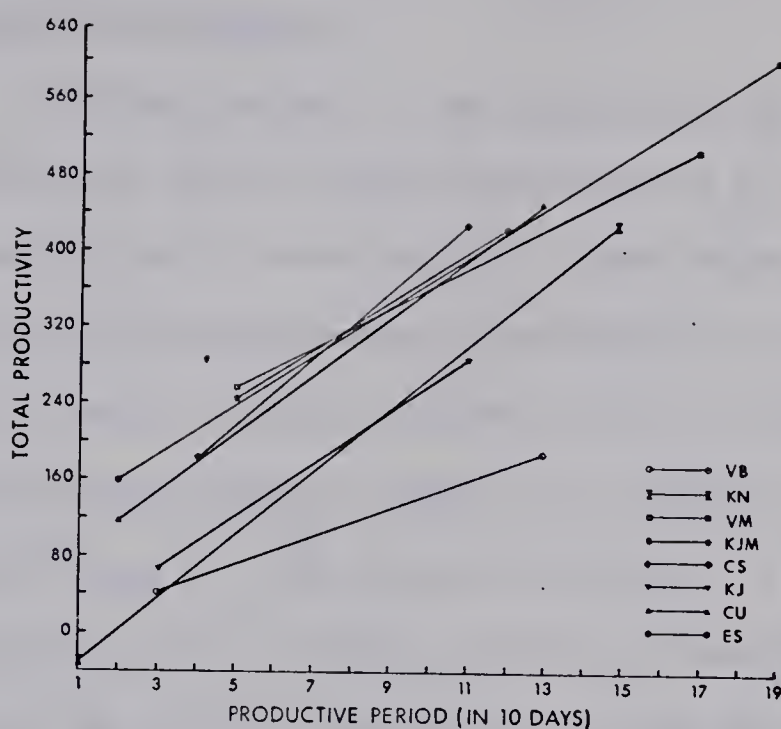


Figure 16. Regression of total productivity on length of period of productivity of the eight populations of T. castaneum used in the analyses of variance (see Table 1 for population identification).

Although there was no consistent relationship between productivity and development, selection for developmental rate by Englert (1964) resulted in a decline in reproductive fitness in his late pupation line and an increase in his early pupation lines. The decline was attributed to both a lowering in fecundity and hatchability. Dawson (1966) reported that selecting for slow development in T. castaneum resulted in a large decrease in hatchability, larval survival and reproductive rate (number of eggs/female/day). Similar significant results are observed here for KJ (Table 6 Appendix) which had the longest developmental time and the smallest productivity suggesting directional selection for longer developmental time in this population.

III. Geographical Clines

The main purpose of the experiment was to determine the differences, if any, among populations of T. castaneum used in genetic and ecologic investigations. Some indication as to whether there were relationships between environmental gradients such as latitude or annual average isotherms could be obtained because the populations were originally chosen from different localities of the world (Figure 4). The populations (Table 1) were grouped in four categories: (1) American (CU, KJM, VM and VB); (2) European (ES, LE, MS and LP); (3) African (CS, KN and MK) and (4) Asian (KJ).

A. Latitude:

1. Body weights: The body weight means (Table 2, Appendix) are plotted according to latitude in Figure 17. American populations had a tendency for body weight to increase as latitude increased, this being quite consistent for pupal and adult weight.

Two of the three African populations (MK and KN) may also show the relationship of body weight increasing with latitude, however, because there are only three points in the African group it is not possible to say which of the populations is the deviate. Assuming the same relationship for the African populations as the American populations then the possibility exists that by sampling error a non-representative sample of CS which does not follow the trend was obtained.

The European populations followed a different trend. Adult and pupal weight decreased in body weight as latitude increased, however, for larval weight there appears to be no relationship with latitude.

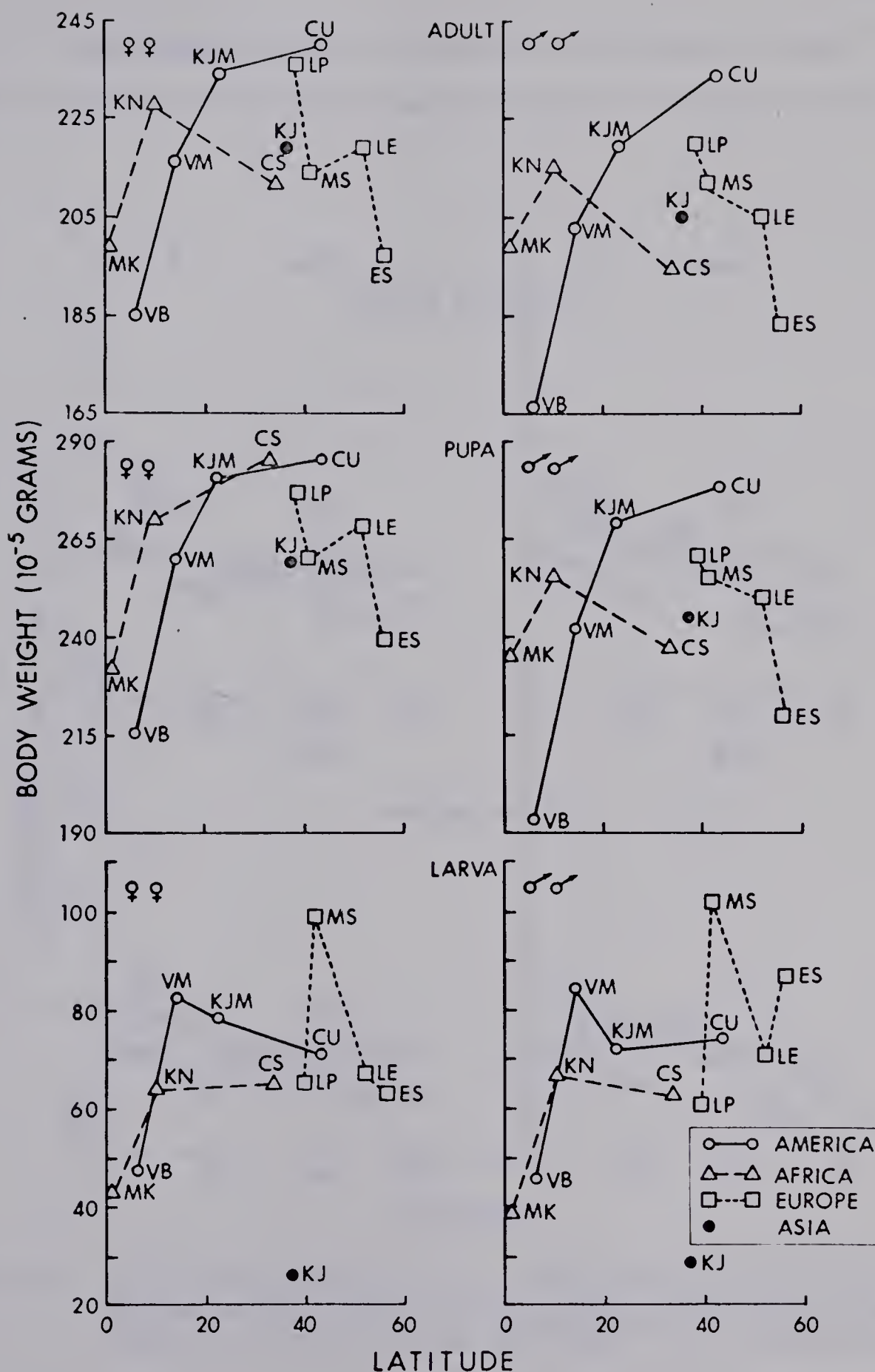


Figure 17. Relationship between body weights and latitude of the twelve populations of *T. castaneum* (see Table 1 for population identification).

2. Developmental times: The means for developmental times (Table 3, Appendix) are plotted against latitude in Figure 18 for

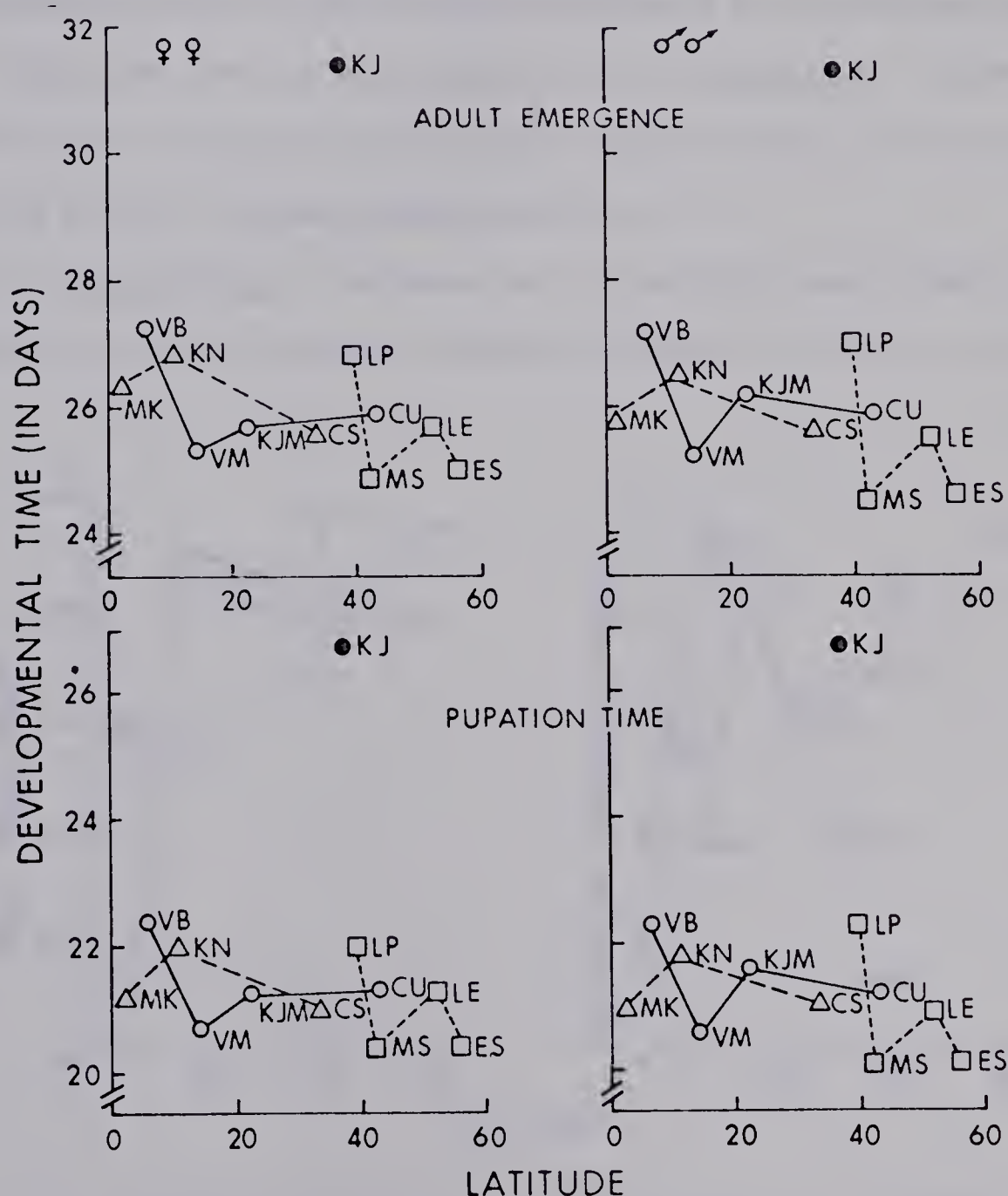


Figure 18. Relationship between developmental times and latitude of the twelve populations of *T. castaneum* (see Table 1 for population identification and Figure 17 for classification).

the four categories. The developmental times of most American, African and European populations showed a tendency toward decreasing

as latitude increased, although there were deviations. Such deviations may have been due to deviation of environmental gradients from the general trend for the other populations. VM may have been influenced by being originally collected from a food substance (corn-meal) different from the most common food for *Tribolium*. Also MK may have been influenced by being only replicated once and therefore, expected to have a larger sampling deviation.

3. Productivity: The means for productivity traits (Table 4, Appendix) are plotted against latitude in Figure 19. Within each

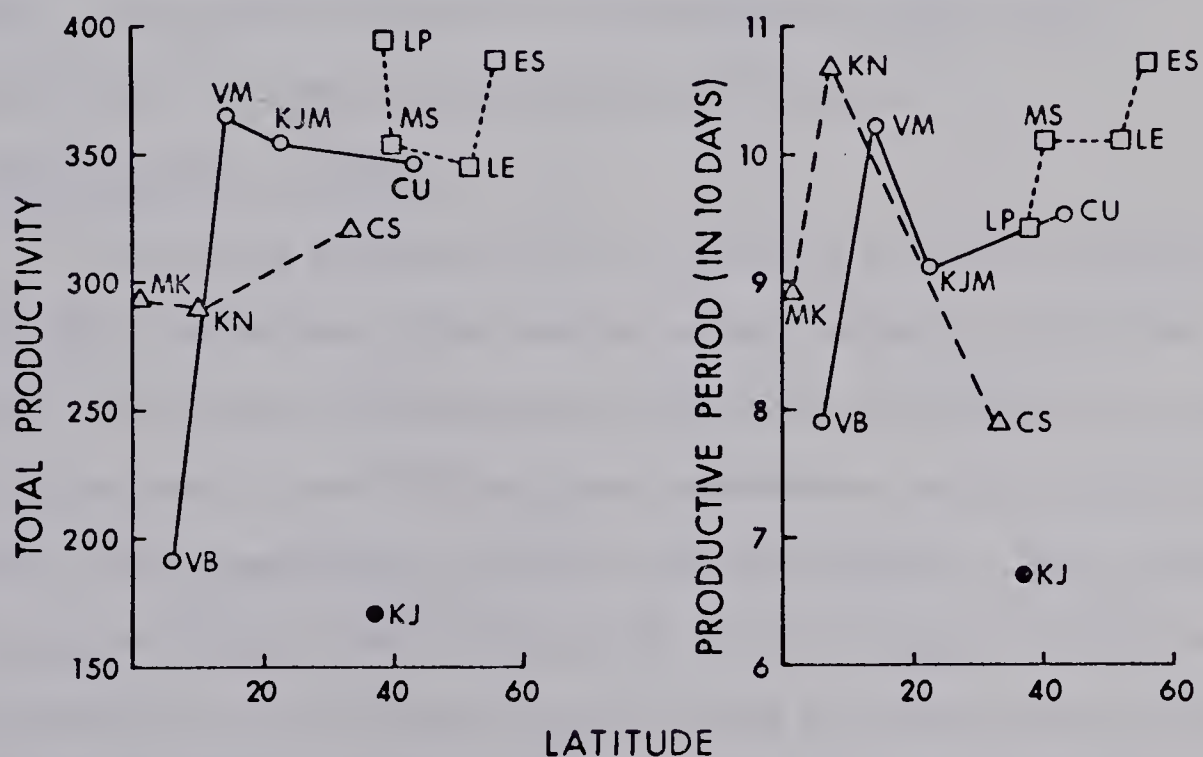


Figure 19. Relationship between productivity traits and latitude of the twelve populations of *T. castaneum* (see Table 1 for population identification and Figure 17 for classification).

group the relationship between productivity and latitude were less consistent than between body weights or developmental times and

latitude. Although American and African populations generally showed a trend toward increasing their productivity with increasing latitude, the relationship for European populations was not as clear. African populations as a group were generally less productive than European populations. Generally populations near the equator were less productive than those away from it.

Period of productivity showed no consistent trend over continents. However, in the European group period of productivity increased as latitude increased. The American group also shows period of productivity increasing with latitude, if VM is not considered. One possible reason for excluding VM is that it was collected from a different food substance (Table 1).

B. Annual average isotherm:

The twelve populations were classified into three groups 8, 17, and 25°C, according to the average annual isotherm of the location from which they were originally collected. The populations plus the weighted mean of each of the three temperature groups are plotted for body weight measurements (Figure 20), developmental times (Figure 21) and productivity traits (Figure 22). Considering all traits the KJ population was so different from the other populations that it was not included in the weighted mean.

1. Body weights: There were graded differences in body weight measurements associated with the locality temperature (Figure 20). Populations from cold localities generally had larger body weights than those from warm localities. Even though European populations showed a reverse pattern with latitude (Figure 17) their inclusion

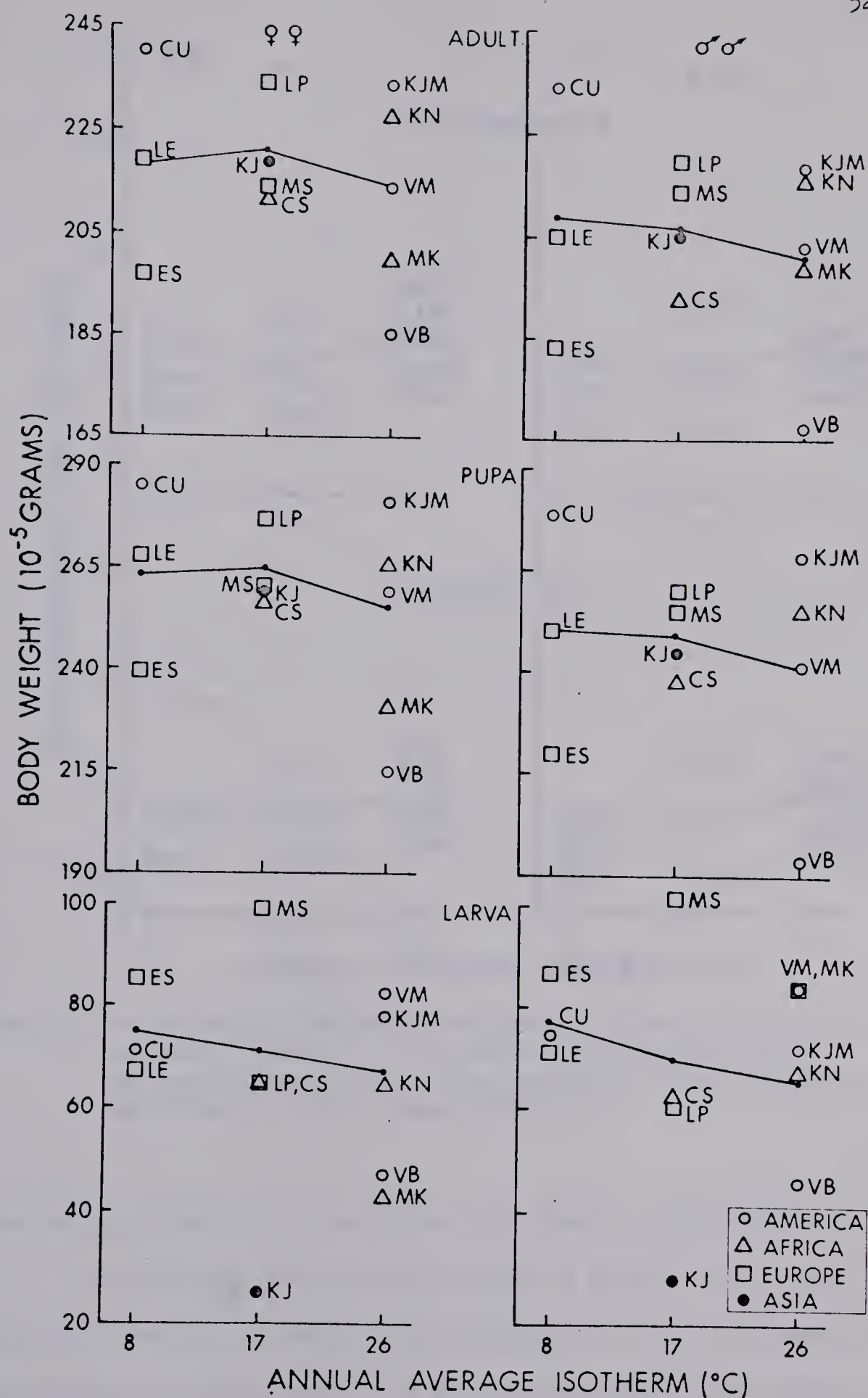


Figure 20. Relationship between body weights and annual average isotherm of the twelve populations of *T. castaneum* (see Table 1 for population identification).

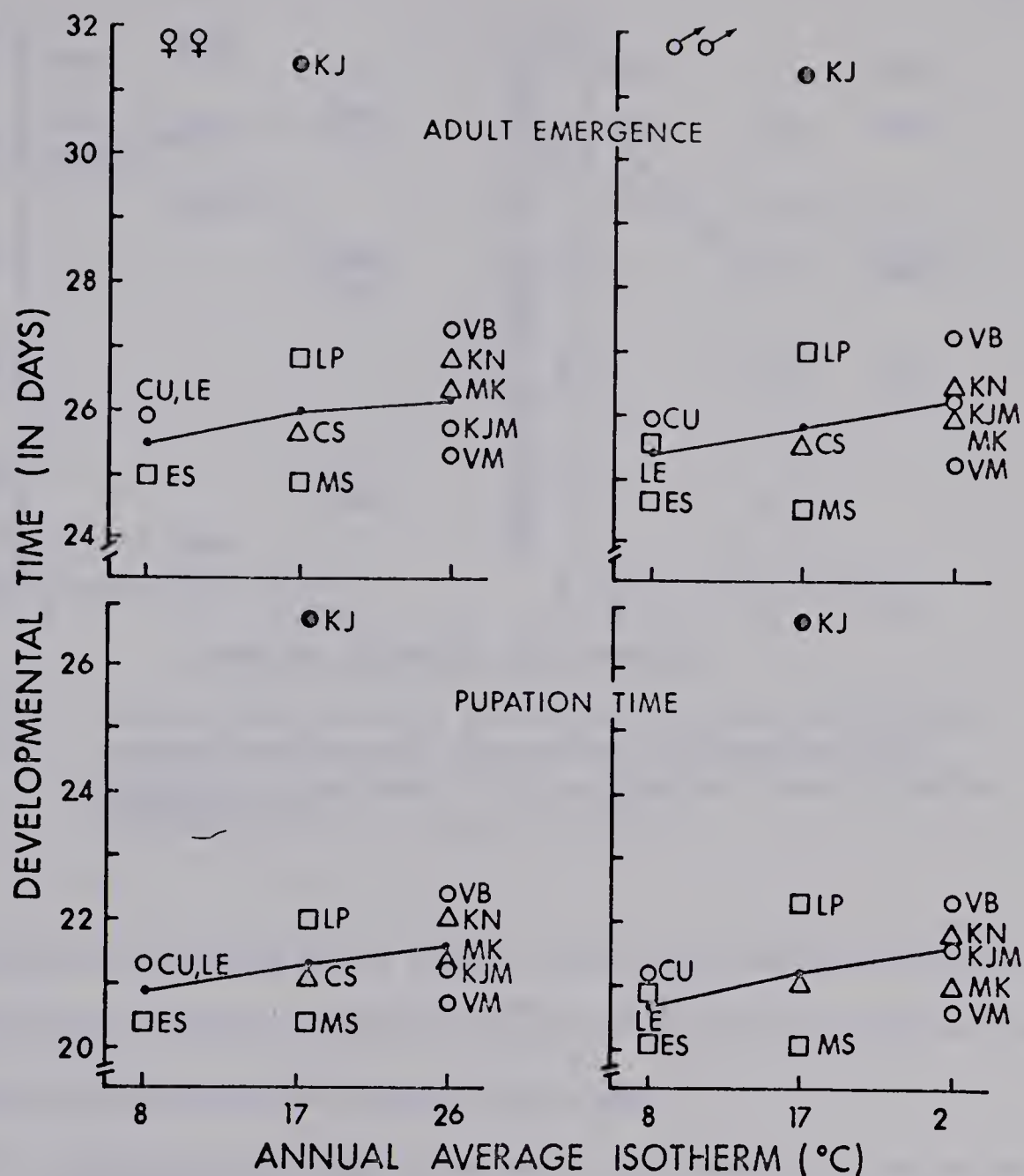


Figure 21. Relationship between developmental times and annual average isotherm of the twelve populations of *T. castaneum* (see Table 1 for population identification and Figure 20 for classification).

in the weighted means does not alter the general relationship.

Similar results have been found by Stalker and Carson (1947), who reported that individuals of *D. robusta* from a cold climate are characterized by longer wings and femora than those from a warm climate. Also Tantawy and Mallah (1961) found that populations of *D. melanogaster* and *D. simulans* from a cold geographical region

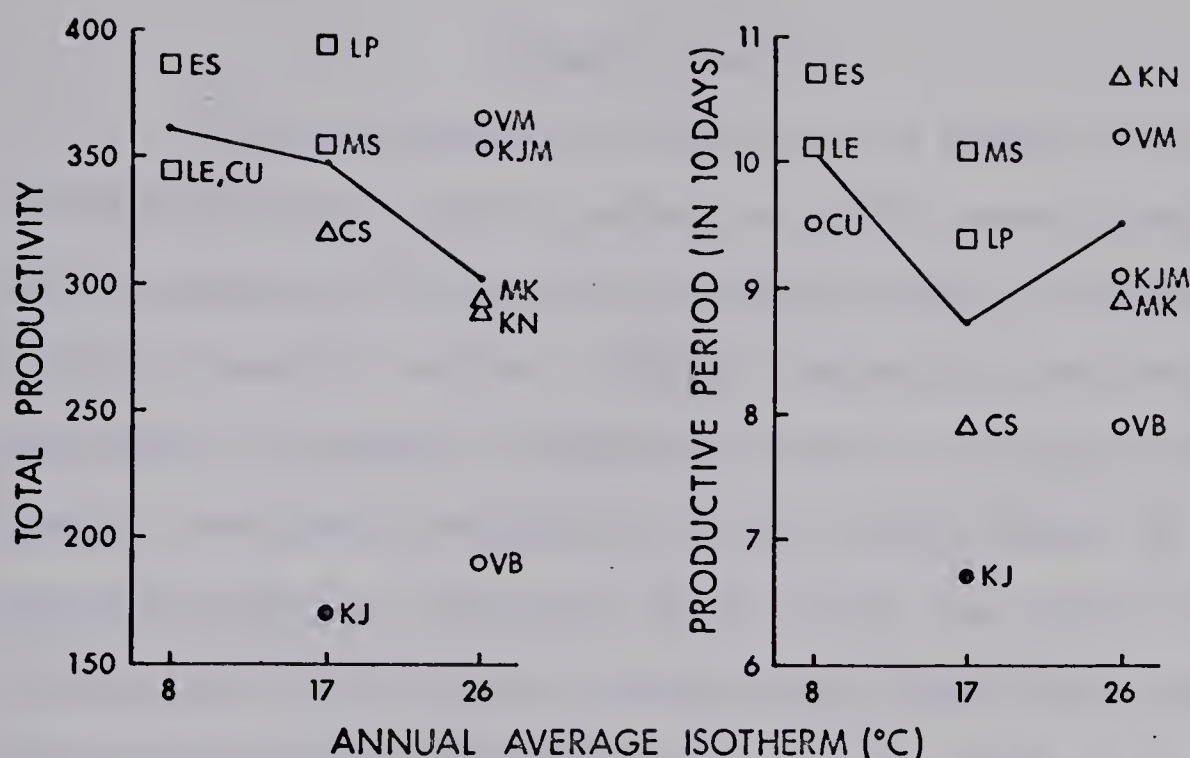


Figure 22. Relationship between productivity traits and annual average isotherm of the twelve populations of *T. castaneum* (see Table 1 for population identification and Figure 20 for classification).

(Lebanon) are morphologically larger than those from a warm region (Uganda) when reared at low experimental temperature, however, the situation was reversed at higher temperature.

2. Developmental times: Both males and females of the twelve populations from colder geographical regions have shorter developmental times (Pt and At), than those from warmer regions (Figure 21).

3. Productivity: The reproductive potential of populations derived from colder geographical regions was greater than those from warmer regions (Figure 22). Period of productivity was longest for populations from cold localities and shortest for populations from the warmer groups. However, for period of production, the mean value for the 17°C populations differed from the relationship indicated by the two extreme temperatures.

GENERAL DISCUSSION

Although geographical variation has a genetic basis, assumed to have been brought about by natural selection, genetic factors have not been seriously considered in ecological studies nor environmental factors in genetical studies. A better understanding of geographic adaptations is possible if discussed in terms of ecological genetics (genetic, environment and gene-environment interaction) of the species. Tribolium castaneum, used in the present study, has several desirable features toward such a better understanding, some of which are: wide distribution, extensively studied ecology and an increasing amount of information on its genetic make-up and gene-environment interaction.

I. Population Differences

Body weights of T. castaneum (Table 5) differed considerably among the populations. Chance occurrence of such differences may arise, where random genetic drift has an effect on the populations, and where the gene pools reorganize during adaptation to different environments. Therefore a slow gradual environmental selection may act to produce gradual genetic divergence of the populations.

Although geographical gradients in body size have not been described in T. castaneum they have been described in several other groups, such as Drosophila. Body size among populations raised under the same conditions, generally parallel the temperatures at which the Drosophila were developed. Flies from cooler regions tend to be larger than flies from warmer regions. Also Drosophila raised at low temperatures are larger than those of the same strain raised at high temperatures (Anderson, 1966 and Tantawy, 1961). In T. castaneum low

temperature and high humidity during development lead to an increase in weights (Howe, 1956).

Although temperature may be the most important selective factor in nature affecting body size, many other factors may complicate and even obscure the formation of a clear gradient. For example, Karten (1965) studying the genetic dimension of T. castaneum environment where the type of food was the variable factor, found that homotypic (media conditioned by the same genotype) and heterotypic conditioned flour (media conditioned by different genotype) differed in their effect on the dry weight. Gene-environment interactions have been found for T. castaneum, e. g., Bray et al. (1962) found that the Purdue foundation stock weighed more in the wet (70% R.H.) than in the dry (40% R.H.) environment. After selection, the large line weighed more in the dry than in the wet environment. As some of the initial families weighed more in the dry than in the wet, it can be assumed that the original population contained the basis for this interaction of the directionally selected lines with the environment.

The major source of variation for developmental rates, pupation time and adult emergence time was due to differences among populations (Table 7). Such variation may have been caused by genetic diversity, environmental factors or the interaction of both. Dawson (1965a, b) found developmental rate (measured as days from egg to pupa) was under genetic control in Tribolium and was an important component of its fitness, being maintained at an intermediate phenotype in nature.

The most important environmental factors which affect the development of T. castaneum are temperature and humidity. Park and Frank (1948), and Howe (1956), found that at constant temperatures development is quickest at the highest humidity used (90% R.H.) and for different humidities at 35°C. In nature temperature is not constant. Messenger and Flitters (1959) showed that wide fluctuations of temperature enable the egg to develop while the mean temperature is still too low. Also the normal deleterious effect of high temperatures are masked because the insects do not suffer continuous exposure to such super-optimal temperature. Since for so many insects, the constant temperature optimum is higher than that which normally occurs, developmental differences among populations may have arisen from selection of strains increasing most rapidly in variable temperatures.

Several investigations have been reported on influence of source of food on larval development of T. castaneum, (Good, 1936; Miller, 1944; Mickel and Standish, 1947; Magis, 1954; Khalifa and Badawy, 1955; and Sokoloff et al. 1962, 1966a, b). Such differences may have been a factor in creating the observed population differences. Except for VM which was collected from white corn flour (Table 1) there is no record available concerning the type of food from which the present populations were collected. As Tribolium reared on corn develop slower than those reared on wheat (Khalifa and Badawy, 1955; and Sokoloff 1966a, b) this may have influenced the development of the VM population when grown on a different medium.

Although no record is available for the other populations, it is possible to speculate on the most likely food for some of the

populations. As it was collected from Japan a probable natural food for the KJ may have been rice. It has been shown by Magis (1954), Khalifa and Badawy (1955) and Sokoloff et al. (1966a, b), that development of Tribolium is slower on polished or brown rice than any other common food. This may have influenced the geographical variation associated with the differentiation of the KJ population. Although after collection, VB and the two populations LE and LP were reared in whole meal, the fact that VB differed from LE and LP, suggests that in their original habitat VB may have been reared on different foods than LE or LP or it may have been subjected to some other environmental differences.

Dawson (1965b) observed significant genotype - environment interaction for developmental rate (from egg to pupa) at 40, 60 and 70% relative humidity. Karten (1965) found that conditioning the flour caused a sharp increase in developmental period of all genotypes studied. Under extreme conditioning the heterozygote and wild type beetles had the higher adaptive values in hetero- and homo-typic conditioned medium.

There was very little variation of pupal period among populations (Table 7). This may indicate that pupal period is not affected by environmental conditions. Good (1936), Gray (1948), Park and Frank (1948) and Kenington (1953) found no effect of temperature on the variation among populations of Tribolium on the duration of the pupal period. Such results agree with those reported in the present study at 33°C. Also pupal period is not affected by difference in humidity (Gray, 1948 and Howe, 1956) nor by kind of

food (Howe, 1956). Therefore no difference for the duration of pupal stage in T. castaneum would be expected among those populations.

For some populations, e.g. KN, the distribution of body weight is not equal around the mean (Figure 5 and 6). This may be explained by a phenomenon related to the genetic structure of Tribolium, in which two populations with overlapped distribution have been observed for freshly emerged pupal weight and developmental periods in both laboratory (Howe, 1961) and field populations (Howe, 1965) of T. castaneum from Kenya. The tail of the distribution was the heavier population that accounted for about 20 percent of the two populations. Similar results were noted in this study for KN population for all body weight measurements, Figure 5. The evolutionary significance of this polymorphic phenomenon may be to provide a mechanism by which the population could adjust itself to diverse environmental conditions (population buffer).

Genetic and environmental factors which may influence the total growth pattern through their effect on its individual components (weight and development) have been presented and discussed for the different populations. A better understanding may be obtained when such components of growth are brought together in overall growth curves, as presented in Figure 9, where the differences among populations derived from different geographical localities can be observed.

Needham (1964) emphasized that genetic instruction must be included for each level of metamorphosis, from the molecular to the systematic. Some evidence of genes specific to hormonal level of

growth control has been given by Needham (1964) and Williams (1961). Williams reported that all aspects of insect development are promoted by the hormone 'ecdysone' which circulates in the blood and which is responsible for larval molts through a synthetic mechanism already present in the cytoplasm of the larval cells. Another hormone 'juvenile hormone', stabilizes the larva as larva by opposing the flow of fresh genetic information from the nucleus to the cytoplasm. Differences in such hormones may explain the differences in the curves of the different populations of T. castaneum at the molecular level.

Although most genes control developmental processes through pleiotropic effects, many single gene growth mutants have been found. For example, Needham (1942) reported a giant mutant of Drosophila which causes the larvae to continue feeding for a longer time than usual, and to grow unusually large. Extremely large and small larvae were observed in the KJ population.

Populations derived from different geographical regions differ in their productivity, both for total productivity and length of productive period (Table 9). As all populations have been reared under the same environmental conditions, such differences probably reflect genetic differences. Differences in productivity of T. castaneum are known to be under genetic control. Crenshaw and Lerner (1964) found interstrain differences in length of oviposition period, total productivity in 120-day and daily productivity over 40 days. Comparison of mutant and wild-type strains (Park, 1937; Park et al., 1945; Kollros, 1944 and Sokoloff et al., 1965) indicated that homozygous mutants are less productive than heterozygote and wild type. Gene-

environment interactions may occur and magnify the differences among populations. Sokoloff et al. (1965) studied different mutant and wild type T. castaneum strains and found that productivity under optimal conditions was 20-40 times more than under sub-optimal. Differences between strains and environment-strain interactions were highly significant.

The deviation of KJ population from the other populations may have been due to its geographical isolation from the other populations. Genetic drift, inbreeding and selection may have caused reduction in the productivity of this population.

Beside the genetic factors, environmental factors such as temperature, humidity, type and condition of food may influence productivity. Park and Frank (1948) found highly significant differences between the effect of three constant temperatures on the fecundity of T. castaneum. However, Howe (1962) found that although there was a considerable variation in fecundity among females of T. castaneum there was no evidence that temperature affects the total number of eggs laid. However, temperature does have an effect on longevity and consequently affects the length of oviposition period. Also very low humidity reduces the total number of eggs laid because it shortens the length of adult life. Moreover, Erdman (1964) reported that period of productivity responses of T. castaneum are influenced by age, temperature, radiation and their interaction and as these factors may differ between populations this may allow differential selection to occur.

Type and condition of food may influence the reproductive performance of a given population in its natural environment. However, the productivity of VM population which had been collected from white corn flour was 367 and that of LE and LP which were reared in whole meal before the experiment started was 346 and 394 respectively (Table 4, Appendix). Good (1936) showed that the oviposition medium influenced the total number of eggs obtained from individual females. His results ranged from an average of 19 eggs per female in white flour to 518 on whole wheat flour. Khalifa and Badawy (1955) obtained an average of 516 eggs per female on whole wheat flour under room conditions. In the present study ES population gave the highest average number of offspring (387) and KJ the lowest (170). As all the populations used in the present study were reared under the same environmental conditions the differences among the populations should be mainly genetical, although the response of the populations may have been conditioned by previous diet.

Recently Sokoloff et al. (1966a, b) determined productivity for T. castaneum on a variety of different media. They found that productivity on corn was greater than on whole wheat flour, which in turn was greater than on white wheat flour. This relationship parallels the amount of leucine, alanine and aspartic acid present in these media. They also showed that the addition of vitamins to corn flour or whole wheat flour stimulated productivity for T. castaneum. The evidence would favor the hypothesis that different geographical populations would respond differently to different media particularly media which differ markedly from their natural food.

Gene-environment interaction has been demonstrated for T. castaneum for productivity, measured as number of pupae and number of pupae and larvae, under two environmental conditions (33.3°C, 45% R.H. and 22.2-26.7°C, 30-35% R.H.) by Kidwell et al. (1964).

Robertson (1957) working on egg production in D. melanogaster suggested that gene-environment interaction will be particularly important under the sub-optimal conditions in which the population usually lives.

The genetic dimension of the environment in regard to the productivity of T. castaneum has been studied. Sonleiter (1961) and Karten (1965) found a significant drop in fecundity of beetles in conditioned flour. Hetero-typically conditioned flour reduces the oviposition rate of the wild type beetle more than the homo-typically conditioned flour.

It is suggested that the productivity of Tribolium populations cannot be specified generally but only for a given set of conditions. Productivity is subject to variation arising from genetic differences among populations, differences among environments and differences in population response to different environments.

The populations differed for phenotypic variance (measured as the coefficient of variation) of weight, development and productivity traits, there being large variability for larval weight (Figure 10) and productivity traits (Figure 12). Such traits are affected by environmental factors more than are developmental times (Pt, Dp and At) and other body weight measurements (Pw and Aw). Environmental fluctuations e.g. temperature, humidity and habitat, which influence larval

weight and productivity may interact with the genetic composition of the population resulting in directional selection in a specific environment.

Variability is usually regarded as a measure of homeostasis on the assumption that a less variable phenotype indicates superior homeostatic buffering properties (Lerner, 1954). Homeostatic buffering results in a high general adaptiveness to a wide range of environments (Lewontin, 1957). Tantawy (1961) found that variability between replicates and individuals within temperature showed that the greater fitness is associated with low variability. The superior genotype at any given temperature produces less phenotypic variability both for fitness components (fecundity) and for metric characters (longevity). While variability between temperatures showed that the poorest genotype has the lowest coefficient of variability or may be equal to the best (heterozygous). Therefore, great care must be exercised in the interpretation of variability as an index of buffering (fitness). Therefore one may postulate that MK and KJ populations may be more adapted to wider changes in environmental conditions than that of VM and MS populations, a point which may be of interest for further study. However, the differences in variability among the populations may have arisen because of natural selection mediated through simple environmental differences.

Information concerning factors which may influence variability through natural selection has come from studies of artificial selection experiments. Falconer (1955) using mice, Reeve and Robertson (1953) and Robertson (1955) using Drosophila, selected

for different quantitative traits and found that the variation in most of the selected lines had increased over the unselected lines. Dawson (1965a) selecting for slow pupal development found that in the unselected control population the coefficient of variation was 10.8 and for the selected populations was 26.3 percent. Moreover, Park and Davis (1945) found that coefficient of variation increased from 16.7 percent for the parental generation to 23.4 percent for the high strain and 31.0 percent for the low strain after 3 generations of selection for fecundity in T. castaneum. Therefore changing the gene pool results in a change of the phenotypic variance.

Because all populations were reared under the same environmental conditions, there should not be any major environmental differences. However, as the populations originated from different parts of the world there could have been an interaction of the environmental factors with the genetic composition of the population resulting in differential responses to natural selection. Such can be inferred from the study of Bray et al. (1962) who suggested that the apparent differential response to selection for pupal weight in the Purdue synthetic population of Tribolium may have been due to the large variance in the dry environment.

II. Relationship Between Traits

Some of the phenotypic correlation coefficients, e.g., (PwxAw), (LwxPt), (LwxAt) and (PtxAt), were quite consistent across populations whereas others were not (Table 12, 13). The consistency of the relations may indicate that genetical control of the traits may be of a similar nature. Such phenotypic correlations do not always match the genotypic relationship and different genetic systems

affecting the physiological mechanism of growth and development may be involved (Englert, 1964). Simpson (1953a), listed some possible mechanisms producing genetic correlation of phenotypic characters, e.g., genetic control of growth patterns (onto-genetic correlation), pleiotropy and linkage.

Several other relationships between the different variables such as (Lw_xPw), (Lw_xAw), (Pw_xPt), (Pt_xAt), (Pt_xAw) and (Aw_xAt) were non-consistent across populations (Tables 12, 13). This may be explained from a genetical point of view as an incidental inclusion of genes in a genetic system integrated on a different basis (Simpson, 1953). However another reason may be derived from selection studies. As most genes seem to affect simultaneously some component of fitness and some more trivial aspect of the phenotype, during selection experiments, normally, correlated response occurs (Mather and Harrison, 1949; Falconer, 1960; Mayr, 1966; and in T. castaneum Englert, 1964). Mather (1940-48) postulated that selection for normally balanced, polygenically controlled characters produce unusual recombinants from crossing over, therefore allowing variation in several characters to occur.

The most interesting relationship between productivity traits and growth traits was between development and total productivity, two important components of fitness. Although the relationships between total productivity and pupation time or adult emergence were not significant for most populations (Table 14) their correlations were negative for most populations. The possible meaning of such negative correlations in natural populations was discussed by Hiraizumi (1961).

In D. melanogaster developmental rate and fertility are negatively correlated within certain range of values. In natural populations the maximum fitness combinations of these two components must be located somewhere in this range. A reduction in one character involves an increase in the other. Thus they compensate within a certain range but beyond that range an increase in one component may become insufficient to compensate for a reduction in the other, resulting in a decline in the total fitness. Hence the more fit genotypes (populations) should have an intermediate level in both components.

The populations studied have been maintained in research laboratories for different periods of time (Table 1) before starting the experiment. Such procedures may be claimed to have brought about changes from those which may have existed in nature in the genetical structure of the populations. Although this may be true, it is assumed in this study that the sample populations studied represent the natural populations from which they were derived.

The reason for this assumption is that these populations have been maintained in the laboratories at optimum or near optimum temperature and humidity conditions. Competition and inbreeding had been kept to a minimum and no directional selection practised. Dawson and Lerner (1962) obtained a response to selection for developmental rate in one inbred line of T. confusum after 13 generations of inbreeding, indicating that characters which are major components of fitness might be expected to possess strong heterotic systems. Levene and Dobzhansky (1958) found that strains of D. pseudoobscura and D. persimilis kept in the laboratory for a period of 130 to 211

generations maintained chromosomal polymorphism. Levene et al. (1965) found that segregational load is more important than mutational load in T. castaneum, and despite 32 generations of inbreeding unexpected amount of concealed variability was found. Lewontin and Hubby (1966) indicated that the amount of heterozygosity present in natural populations may be much greater than has previously been suspected. However Dawson (1965a) hypothesized that developmental rate in Tribolium has an intermediate optimum, possibly as a result of superiority of heterozygotes with regard to fitness. Such superiority of heterozygotes provides a mechanism for maintenance of genetic variability which protect the population against environmental fluctuations (Lerner, 1954). Natural selection, in outbreeding populations, acts as a stabilizing force for the intermediate heterozygote types (Dawson, 1968), and is directed to maintain a canalized developmental pattern (Waddington, 1957) which provides the population with greater phenotypic stability.

III. Geographical Clines

The results for different geographical populations appear to show geographic clines for both latitude (Figure 17, 18 and 19), and annual average isotherm (Figures 20, 21 and 22) for some traits studied for both males and females. These results were obtained even though T. castaneum is a species which is known to be associated with human activity and frequently to live in semi-controlled conditions.

The data presented showed that; in general, larval, pupal and adult weights of T. castaneum derived from different geographical regions in Africa and America (Figure 17) increase with increasing latitude or decrease with annual average isotherm (Figure 20).

These results agree with Bergmann's rule. A trend to increase body size with increasing latitude (which correlates with the average annual temperature of the same localities) was found by Stalker and Carson (1947), Prevosti (1955), Tantawy and Mallah (1961) and Misra and Reeve (1964) for different species of Drosophila. Flies from cooler regions were found to be larger than those from warmer ones. On the other hand, there was no evidence of a general cline in size correlated with latitude over the range of D. pseudoobscura studied by Sokoloff (1965), where the complex range of the territory which D. pseudoobscura inhabits may obscure such a correlation. This may partially explain the results reported for the European group (Figure 17), the range of territories of which is smaller.

Evidence for the selective effects of temperature in natural populations has come from laboratory experiments. Investigators who kept animals in laboratories at different temperatures found that larva (Imai, 1937) wing, tibia and thorax length (Alpatove and Pearl, 1929 and Eigenbrodt, 1930) are larger at low temperatures than higher ones. Reed and Reed (1948) studied the wing length of three closely related species of Drosophila; namely, pseudoobscura found in the warmest regions, persimilis found in intermediate regions and miranda found in coldest regions. Pseudoobscura has the shortest wing length and miranda has the longest. Such observed genotypic

changes were shown by Ray (1960) to have a phenotypic parallism in the change of wing length of female pseudoobscura and persimilis at 13, 16, 19 and 24°C. Pseudoobscura was shown to have shorter wings than persimilis at each of these temperatures. This reveals the adaptability of wing length to environmental temperature at a species level. Ray (1960) raised four species of Drosophila (willistoni, equinoxialis, pseudoobscura and persimilis) collected from a single locality at temperatures varying between 16°C and 29°C. For each species there were striking increases in size, as measured by either wet body weight or wing length, at successively lower temperatures. Tantawy and Mallah (1961) found that both D. melanogaster and D. simulans populations from a cold region (Lebanon) were larger in body size than populations from a warmer region (Uganda) at low temperatures (10-15°C) but the situation is reversed at the higher temperatures (25-30°C).

Further evidence of the genetic bases of population adaptation to environmental temperatures comes from Vetukhiv's experimental populations (Anderson, 1966). The populations kept at lower temperature for 6 years have genetically larger flies than the populations kept at higher temperatures. Such results are supported by those of Druger (1962), who selected for body size in D. pseudoobscura at different temperatures. A similar behaviour was shown by Vetukhiv's populations, which have undergone natural selection for body size and Druger's artificially selected lines (Anderson, 1966).

This size temperature relationship may be explained by two phenomena; (1) shifts in the metabolic balance at different temperature

levels (Imai, 1937 and Ryan, 1941), or, (2) delayed ontogeny (Wimpenny, 1941). The present study showed that developmental rate which is negatively correlated with body weight (Figure 14) decreased with an increase in the annual average isotherm (Figure 21). Englert (1964) computed the correlation between the mean of body weights (larvae, pupae and adults) and development (pupation time and emergence time) across populations (genetic correlation in a broad sense). He found that an inverse relationship between 13-day larval weight and pupation time ($r = -.51$) and an inverse relationship between larval weight and emergence time ($r = -.22$) existed.

A mechanism for the transfer of phenotypic characters into the genotype called the "Baldwin effect" which could account for the parallel between environmentally induced change in the phenotype and genotypic differences was proposed by Simpson (1953b) and Waddington (1953 and 1961). Evidences indicating that the Baldwin effect may be widely operative has come from the existence of genotypic and physiologic races associated with temperature and latitudinal differences (Bullock, 1955 and Prosser, 1955).

Latitude and environmental temperature are not equivalent. Differences in micro-environmental temperatures which are difficult to measure tend to obscure geographical clines. Behavioral thermoregulation for flour beetles makes it difficult to correlate body temperature with environmental temperature, as hot spots embedded in very cold grain have been found in farms and warehouses (Howe, 1965). Because the smaller the surface/volume ratio is, the lesser will be the heat dissipation, experimental work relating heat conservation,

size and metabolism will increase our understanding of the problem and test the universality of ecological rules such as Bergmann's rule. Moreover, while annual temperature is the most obvious detectable environmental factor which shows a correlation with morphology, it is not the only factor that controls and influences size. Some other factors may make smaller size of greater adaptive value, e.g. food, competition, behaviour temperature regulations, humidity or the interaction between any of these factors as is the situation in most cases in nature. Body size is to a great extent the result of a complex interaction between environmental and specific hereditary factors, rather than a direct adaptation to specific environmental conditions. Although the phenotypic effect of experimentally controlled temperature has been clearly demonstrated, other factors confuse the picture in nature. It remains to be determined exactly how the basic relationships might have been altered genotypically through selection (Ray, 1960). Thus the apparant outstanding position of KJ population may be a reflection of a change in some environmental factor of which we have no knowledge and needs to be further investigated.

The data presented for population differentiation indicate that although T. castaneum lives in a semi-controlled environment and its microenvironment and behaviour may interact and obscure population differences, still differences in its quantitative traits are demonstrable. However, it is possible that the observed phenotypic differences may be less than expected, as experimental conditions were controlled while in nature they vary considerably. Even though for those populations which show a high degree of phenotypic

similarity, it still could be argued that this similarity is a result of developmental homeostasis and not a reflection of real genetic similarity.

The demonstration of geographical clines indicates that geographical variation of the species, which is brought about by natural selection, is the inevitable consequence of geographical variation in the environment, as pointed out by Huxley (1954), Mayr (1942 and 1966), Dobzhansky (1951) and Rensch (1947 and 1960).

It is suggested that populations of T. castaneum are divided into many demes (partially isolated, natural or experimental populations) which gradually diverge in their genic composition forming distinct gene pools. Polygenes controlling components of growth and productivity may be maintained in a heterozygous condition thereby providing the population with a buffering mechanism against environmental stresses and enabling the species to exploit a wider range of niches (see Sokoloff, 1965 for further discussion).

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APPENDIX

Table 1: Sources of populations studied.

Code	Population	Source
1.CU	Chicago, U.S.A.	T. Park Department of Zoology University of Chicago Chicago, Illinois.
2.CS	Capetown S. Africa	A. Bell Population Genetics Institute Purdue University Lafayette, Indiana.
3.KJ	Kyoto, Japan	
4.VB	Vicosa, Brazil	
5.ES	Edinburgh, Scotland	L. Sparrow Department of Agriculture and Fisheries for Scotland, Agriculture Scientific Services Edinburgh, Scotland.
6.KN	Kano, Nigeria	F. Waterhouse Department of Natural History Queens College Dundee, Scotland.
7.MK	Makakos, Kenya	
8.KJM	Kingston, Jamaica	
9.LE	London, England	G. Brett Infestation Control Laboratory Tolworth Surbiton Surrey, England.
10.LP	Lisbon, Portugal	C. Baeta-Neves Laboratorio De Defesa Fitossantitaria Dos Productos Armazenados Lisbon, Portugal.
11.MS	Madrid, Spain	F. Orozco Instituto Nacional De Investigaciones Agronomicas Madrid, Spain.
12.VM	Veracruz, Mexico	A. Sokoloff Department of Genetics University of Berkeley Berkeley, California.

Table 2: Body weights (10^{-5} grams) of the twelve populations.

Popula- tion	Weights							
	Larvae		Pupae			Adult		
	Mean	S.E.	Mean	S.E.	N	Mean	S.E.	N
Males								
CS	62.6	2.7	237.4	4.2	72	195.0	3.4	71
CU	74.1	3.8	278.3	3.1	78	233.9	2.9	77
ES	86.6	3.8	220.4	3.4	70	182.7	3.0	68
KJ	29.1	1.7	244.6	3.9	65	205.0	2.9	64
KJM	71.9	4.4	265.0	2.9	70	218.9	2.6	70
KN	67.3	2.6	259.8	3.2	75	215.0	2.7	75
LE*	70.9	3.2	250.3	3.0	61	205.5	2.4	61
LP*	61.2	3.0	261.2	4.2	50	219.8	4.0	49
MK*	38.5	4.7	235.9	7.3	15	198.5	4.7	14
MS*	101.7	5.6	255.9	5.3	32	212.1	4.5	32
VB	46.4	2.4	193.4	2.7	70	166.5	2.4	67
VM	84.2	2.7	242.3	3.9	78	201.7	3.3	75
Females								
CS	64.8	2.7	257.1	3.7	75	212.4	3.1	75
CU	70.9	2.9	285.0	3.6	69	239.6	2.9	66
ES	85.3	3.5	238.6	3.3	79	196.6	2.9	79
KJ	26.4	1.6	259.2	3.6	72	218.9	2.8	72
KJM	77.6	3.7	280.6	3.0	78	234.3	3.0	78
KN	64.0	3.0	270.4	3.8	67	228.1	3.0	67
LE*	67.4	3.2	267.7	3.5	57	218.6	2.7	57
LP*	64.8	2.9	276.9	3.1	67	236.2	3.0	66
MK*	43.0	5.4	231.6	5.4	10	198.5	5.8	10
MS*	99.1	6.0	260.4	4.5	28	214.3	3.7	28
VB	46.7	2.2	216.6	2.9	75	185.2	2.5	74
VM	81.6	2.6	258.6	4.0	71	216.2	3.4	71

* Populations which had less than five replicates and not used in the analyses of variance.

Table 3: Developmental times (days) of the twelve populations.

Popula- tion	Pupation time		Duration of Pupal Stage			Adult emergence time		
	Mean	S.E.	N	Mean	S.E.	Mean	S.E.	N
Males								
CS	21.0	.20	72	4.6	.06	25.6	.21	71
CU	21.2	.15	78	4.7	.06	25.9	.15	77
ES	20.1	.13	70	4.5	.08	24.6	.16	68
KJ	26.7	.29	65	4.7	.07	31.3	.30	64
KJM	21.6	.17	70	4.7	.05	26.3	.17	70
KN	21.8	.31	75	4.6	.06	26.4	.29	75
LE*	20.9	.12	61	4.7	.06	25.5	.16	61
LP*	22.3	.20	50	4.6	.06	27.0	.19	49
MK*	21.5	.26	15	4.8	.11	25.9	.51	14
MS*	20.1	.24	32	4.4	.11	24.5	.27	32
VB	22.3	.19	70	4.8	.05	27.2	.20	67
VM	20.6	.15	78	4.6	.06	25.2	.17	75
Females								
CS	21.1	.22	75	4.5	.06	25.7	.23	75
CU	21.3	.13	69	4.7	.07	25.9	.14	66
ES	20.4	.13	79	4.5	.07	25.0	.15	79
KJ	26.7	.28	72	4.7	.08	31.4	.29	72
KJM	21.2	.13	78	4.5	.06	25.7	.14	78
KN	22.0	.19	67	4.8	.06	26.8	.19	67
LE*	21.3	.13	57	4.6	.06	25.9	.14	57
LP*	22.0	.16	67	4.7	.06	26.8	.16	66
MK*	21.3	.25	10	5.0	.15	26.4	.16	10
MS*	20.4	.31	28	4.5	.10	24.9	.36	28
VB	22.4	.16	75	4.8	.06	27.2	.16	74
VM	20.7	.17	71	4.6	.06	25.3	.17	71

* Populations which had less than five replicates and not used in the analyses of variance.

Table 4: Reproductive periods and total productivity of the twelve populations.

Population	N	Productivity			
		Period (10 days)		Total	
		Mean	S.E.	Mean	S.E.
CS	68	7.9	.3	332.4	13.1
CU	59	9.5	.3	345.6	16.5
ES	63	10.7	.3	386.8	15.3
KJ	52	6.7	.3	169.5	14.8
KJM	54	9.1	.2	352.7	16.2
KN	57	10.7	.4	289.6	18.7
LE*	52	10.1	.3	345.9	16.8
LP*	39	9.4	.6	394.2	22.9
MK*	10	8.9	1.6	293.7	70.8
MS*	24	10.1	.4	353.7	12.4
VB	54	7.9	.3	192.6	12.0
VM	60	10.2	.3	365.8	12.4

* populations which had less than five replicates and not used in the analysis of variance.

Table 5: Coefficient of variation of body weight, developmental time and productivity traits of the twelve populations.

Popula- tion	Traits						
	Weight			Time		Productivity	
	Larval	Pupal	Adult	Pupa- tion	Adult emerg.	Period	Total
Males							
CS	36.7	15.2	14.7	8.0	6.9		
CU	45.7	9.8	10.8	6.1	5.1		
ES	36.3	13.0	13.6	5.2	5.4		
KJ	48.0	12.8	11.4	8.7	7.6		
KJM	51.0	9.1	10.0	6.6	5.3		
KN	33.8	10.7	10.8	12.1	9.6		
LE*	34.8	9.3	8.9	4.6	4.7		
LP*	36.1	11.4	12.8	6.4	4.9		
MK*	47.2	12.0	7.8	4.6	6.5		
MS*	31.3	11.7	12.1	6.7	6.3		
VB	26.6	11.9	12.0	7.1	5.9		
VM	27.9	14.3	14.2	6.5	5.8		
Females							
CS	35.5	12.6	12.5	9.1	7.6	27.1	33.4
CU	34.3	10.3	9.8	4.9	4.3	26.0	36.6
ES	36.5	12.3	12.9	5.5	5.5	25.9	31.5
KJ	51.2	11.7	10.8	8.9	7.7	30.3	62.8
KJM	42.6	9.6	11.2	5.3	4.7	19.6	33.8
KN	38.1	11.5	10.6	7.0	5.8	26.2	48.8
LE*	35.8	9.9	9.3	4.6	4.0	21.9	35.0
LP*	36.4	9.2	10.2	5.8	4.9	36.7	36.3
MK*	40.0	7.3	9.2	3.7	2.0	55.5	76.3
MS*	31.9	9.0	9.1	8.0	7.6	21.0	17.2
VB	40.9	11.6	11.4	6.1	5.0	31.6	45.7
VM	27.4	12.9	13.2	6.7	5.6	21.1	26.3

* population had less than five replicates.

Table 6: Linear regression coefficients ⁽¹⁾ b $\pm$ S.E. for traits showing significant correlation

Population	Aw on Pw (2)	Pt on Lw	At on Lw	At on Pt	Tp on Pp
Males					
CS	.73 $\pm$.042	-.04 $\pm$.007	-.05 $\pm$.007	1.01 $\pm$.035	
CU	.81 .047	-.03 .003	-.03 .003	.92 .047	
ES	.76 .051	-.02 .003	-.03 .004	1.07 .081	
KJ	.68 .041	-.10 .016	-.11 .017	1.02 .031	
KJM	.79 .051	-.03 .003	-.03 .003	.91 .038	
KN	.72 .054	-.07 .011	-.06 .011	.93 .023	
LE	.66 .055	-.03 .004	-.03 .004	1.14 .063	
LP	.77 .077	-.05 .006	-.04 .007	.87 .051	
MK	.51 .037	-.04 .010	-.05 .021	1.00 .380	
MS	.79 .058	-.03 .005	-.04 .005	1.05 .082	
VB	.82 .028	-.06 .006	-.06 .007	1.00 .037	
VM	.77 .032	-.04 .005	-.04 .006	1.01 .047	
Females					
CS	.73 $\pm$.047	-.04 $\pm$.004	-.04 $\pm$.005	1.02 $\pm$.052	35.91 $\pm$ 4.27
CU	.67 .052	-.03 .003	-.03 .004	.95 .061	30.75 5.47
ES	.81 .043	-.02 .003	-.03 .004	1.04 .071	26.26 4.55
KJ	.73 .040	-.11 .016	-.11 .016	.96 .037	27.73 6.25
KJM	.83 .083	-.02 .003	-.04 .004	.94 .072	25.94 8.51
KN	.69 .045	-.03 .007	-.03 .007	.93 .040	33.32 5.15
LE	.69 .048	-.02 .005	-.03 .005	.95 .069	20.19 7.17
LP	.62 .128	-.03 .006	-.03 .007	.92 .085	32.47 4.23
MK	.87 .203	-.03 .009	-.03 .005	.74 .176	41.52 6.32
MS	.71 .084	-.03 .005	-.04 .007	1.13 .077	6.40* 5.94
VB	.79 .036	-.04 .008	-.03 .009	.93 .054	24.88 3.49
VM	.81 .047	-.04 .006	-.04 .006	.97 .046	21.12 5.23

(1) all linear regressions are significant at .05 unless specified.

(2) Y on X

* not significant at .05 level of probability.

Table 7: Test of homogeneity of regression lines for the eight populations.

Regression (y on x)	F values	
	Males	Females
Aw on Pw	9.54*	2.10*
At on Pt	1.82	.55
Pt on Lw	9.81*	11.82*
At on Lw	9.39*	9.44*
Tp on Pp	-	.85

d.f. = 7,547 for males and 7,451 for females.

* significant at .05 level of probability.

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